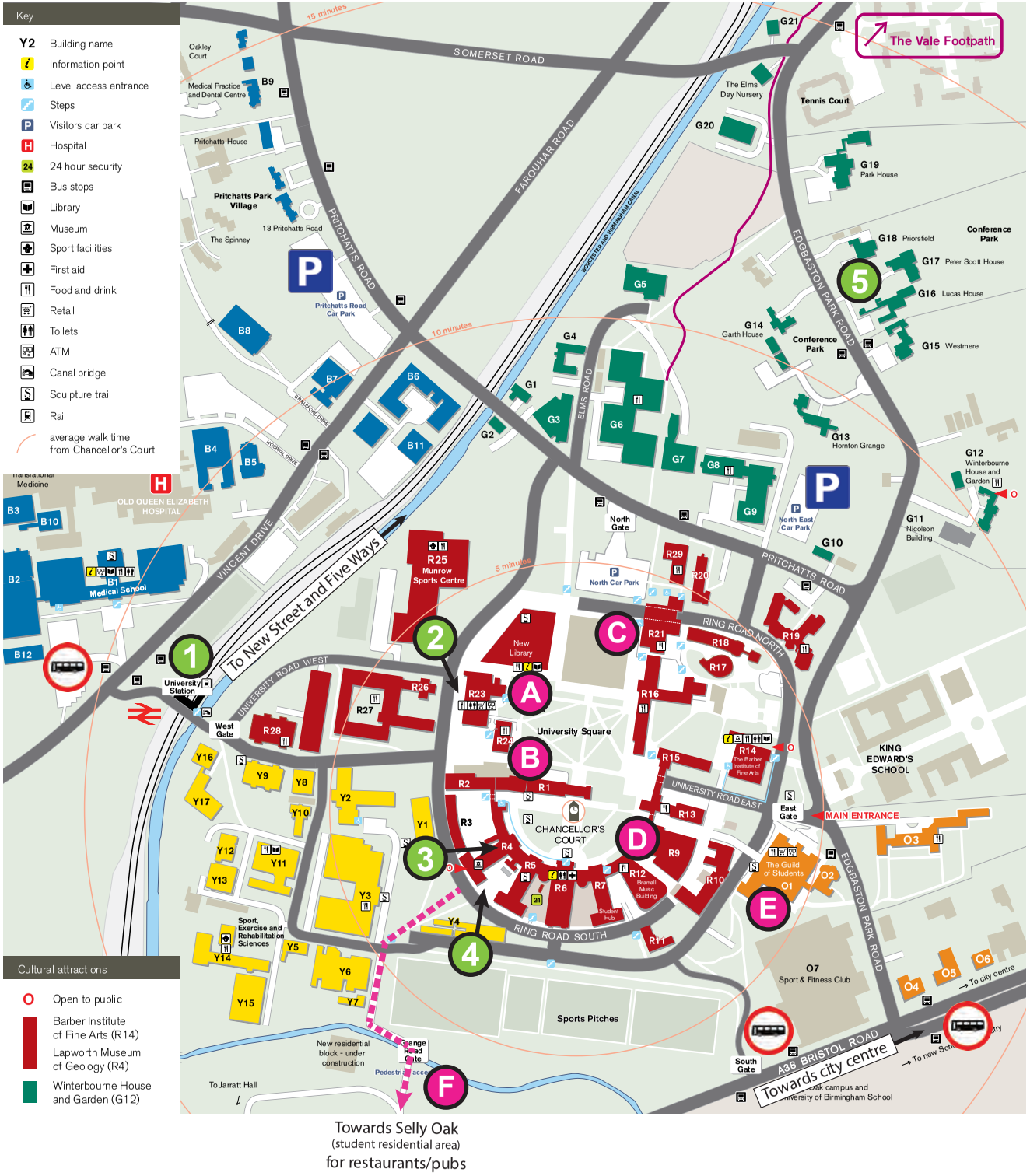
The 65th Symposium on Vertebrate Palaeontology and Comparative Anatomy & The 26th Symposium on Palaeontological Preparation and Conservation

UNIVERSITY OF BIRMINGHAM:
12TH–15TH SEPTEMBER 2017

ABSTRACT VOLUME

SVPCA & SPPC Venues

University of Birmingham
Edgbaston Campus (B15 2TT)



1 University Train Station

2 Avon Room & Lounge (R23)

- Registration (12th-14th)
- Poster session (Wed 13th)
- Platform presentations (12th-14th)

3 Earth Sciences Department (R4)

- Workshops (Tue 12th)

4 Lapworth Museum of Geology (R4)

- Icebreaker event (Tue 12th)

5 Lucas House Accommodation (G16)

Food Outlets on Campus

A University Centre (R23)
- **SPAR** (ground floor) - grocery store serving hot food
- **Café GO** (ground floor) - hot food, sandwiches, and salads
- **COSTA** (access from outside)

B Staff House (R24)
- **Bratby Bar** (ground floor) - hot food
- **Café Aroma** (1st floor) - coffee and sandwiches
- **Noble Room** (2nd floor) - hot food

C Muirhead Tower (R 21)
- **Starbucks**

D Bramall Music Building (R 12)
- **COSTA**

E Guild of Students (O1)
- **Subway** - sandwiches and salads
- **SPAR** - grocery store serving hot food

F Selly Oak pubs/restaurants

P Visitor Parking

Bus stops

Acknowledgements

The organizers would like to thank our generous sponsors—The Palaeontological Association, Wiley, eLife, PLOS ONE, Transmitting Science and PeerJ—for their financial support of the meeting. Many thanks to the members of the SVPCA Steering Group—Peter Falkingham, Richard Forrest, Cindy Howells, Susannah Maidment, Liz Martin-Silverstone, Rob Sansom, and Paul Upchurch—for support throughout, with particular thanks to Richard Forrest for running the SVPCA website and handling the abstract submission process. Finally, thanks to everyone who provided donations to the auction.

Host Committee

Richard Butler (chair), Ivan Sansom, Stephan Lautenschlager, Susannah Thorpe, Roger Close, Plamen Andreev, Daniel Cashmore, Emma Dunne, Pedro Godoy, Andy Jones, Juan Benito.

Student Helpers

Emily Brown, Luke Meade, Kai McWhirter, Alahna Munks, Matthew Scandrett, Kelly Thompson.

Abstract Publication

Abstract authors have been sent instructions via email of how to add their abstract, should they wish to, to a SVPCA/SPPC 2017 proceedings collection at PeerJ Preprints. Presentation slides, posters and resultant papers (if published in PeerJ) can also be added to this collection. The collection can be viewed at:
https://peerj.com/collections/49-svpca-sppc-2017/

Student Presentation Prizes

There will be two student presentation prizes this year. The best student talk (platform or lightning) will win a full author processing charge (APC) waiver for a publication at PeerJ. The best student poster will win a tuition fee waiver for their choice of one of the training courses run by Transmitting Science in Barcelona.

The judges for the prizes will be Rob Sansom, Susannah Maidment, Paul Upchurch, Cindy Howells, and Richard Forrest.

JONES-FENLEIGH FUND

Following review of all applications, the Host Committee decided to this year award four full Jones-Fenleigh (JF) grants of up to £250 each, and four partial JF grants of up to £150 each. Subsequently, a generous donation from PeerJ allowed us to provide partial JF grants of up to £100 each to two further applicants. As such, the JF this year was able to support 10 applicants.

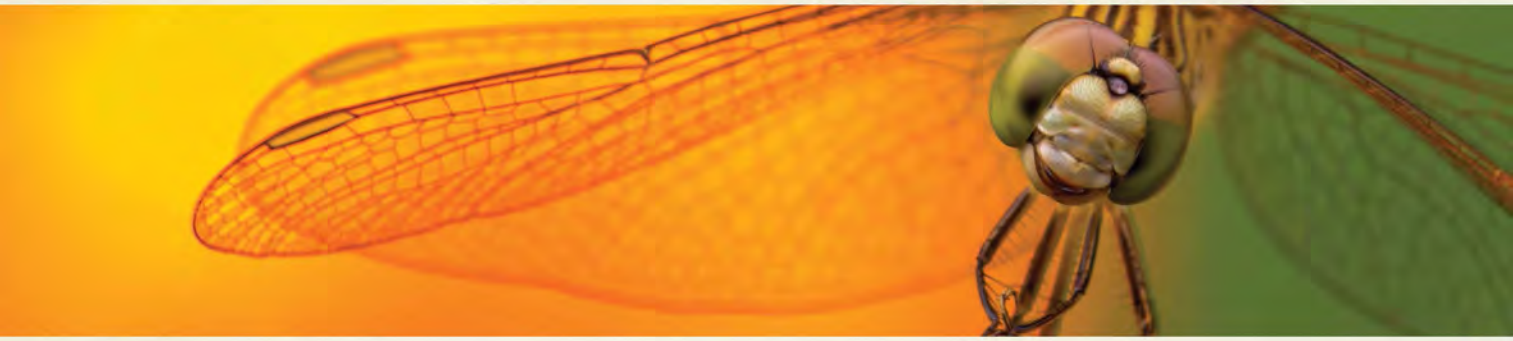
The awardees of the JF grants for 2017 were: Bruno Campos (Karlsruhe), Sally Collins (Birkbeck), Davide Foffa (Edinburgh), Struan Henderson (Edinburgh), Elizabeth Kerr (Paris), Elizabeth Martin-Silverstone (Southampton), Philip Morris (Hull), Emma Randle (Manchester), Aubrey Roberts (Southampton) and Christina Shears-Ozeki (Portsmouth).

LOGO

The logo of the 2017 SVPCA meeting features a pterosaur clinging to one of the faces of the clock of the iconic 'Old Joe' tower, which lies at the heart of the University of Birmingham (UoB) campus. The logo was designed by Plamen Andreev, a postdoctoral researcher in vertebrate palaeontology at UoB, and the pterosaur was inspired by a reconstruction of *Eudimorphodon* by Todd Marshall.

Old Joe is the tallest free-standing clock tower in the world, a well-known landmark in south Birmingham, home to a breeding pair of peregrine falcons, and much loved by UoB students, even having its own Twitter account. The logo also pays an indirect homage to the work of one of Birmingham's most famous literary figures, J. R. R. Tolkien, who grew up in what are now the nearby Birmingham suburbs of Kings Heath, Moseley and Edgbaston, and attended the King Edward's School adjacent to the UoB campus. Tolkien is believed to have drawn inspiration from a number of landmarks in the city when writing his Middle-earth novels, and Old Joe is reputed to have inspired the Eye of Sauron. The fell beast ridden by Sauron's servant, the Witch-king of Angmar, was acknowledged by Tolkien to be 'pterodactylic', much like the pterosaur shown in the logo.

transmitting science



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- Introduction to Ecological Data Analysis. 3rd Ed.
- Introduction to R. 2nd Ed.
- R without Fear: Applied R for Biologists. 3rd Ed.
- A Gentle Introduction to R for the Biological Sciences. 1st Ed.

ECOLOGY

- Introduction to Agent Based-Models Using NetLogo. 4th Ed.
- Integral Projection Models: Demography in a Continuous World. 2nd Ed.
- Introduction to Ecological Niche Modelling. 2nd Ed.
- Comparative Approaches in Ecology, Evolution and Conservation Science. 1st Ed.

GEOMETRIC MORPHOMETRICS

- Introduction to Geometric Morphometrics. 10th Ed.
- 3D Geometric Morphometrics. 7th Ed.
- Morfometría Geométrica para Principiantes. 3ª Ed.
- Geometric Morphometrics and Phylogeny. 8th Ed.
- Integration and Modularity with Geometric Morphometrics. 5th Ed.
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- Mapping Trait Evolution. 2nd Ed.
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BIOGEOGRAPHY

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IMAGING

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- Introducción a las Técnicas de Microscopía: Óptica y Electrónica. 6ª Ed.
- Introduction to Electron Microscopy for Life Sciences. 2nd Ed.
- Introduction to 3D Imaging Technologies: Photogrammetry, Laser, CT-scan and (μ)CT-scan for Life Sciences. 3rd Ed.
- Técnicas Avanzadas de Microscopía de Fluorescencia y Confocal. 2ª Ed.

PALAEONTOLOGY AND ARCHAEOLOGY

- Palaeontology and the Sixth Extinction. 1st Ed.
- Applied GIS: 3D Reconstruction of Archaeological Interventions. 1st Ed.

SYSTEMS BIOLOGY

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DRAWING AND COMMUNICATION

- Introduction to Naturalistic and Scientific Illustration. 4th Ed.
- Interactive Data Analysis and Visualization with R Shiny. 1st Ed.
- Introduction to Bibliographic Search and Management for Life Scientists. 1st Ed.
- The Art of Science: Scientific Illustration. 1st Ed.

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- Fluid Preservation. 1st Ed.

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nature
THE INTERNATIONAL WEEKLY JOURNAL OF SCIENCE
Dinosaur divisions
Family tree gets radically redrawn
PAGES 494 & 501
ASTRONOMY
BLACK-HOLE HUNTER
PUBLISHING
EDITOR VS PREDATOR
Journals offer board jobs to fake scientist
CONDENSED MATTER PHYSICS
GOOD VIBRA

The Early Tetrapod World:
laying the foundations of the modern vertebrate fauna

A one-day conference in honour of

Prof Jenny Clack FRS,

to mark her formal retirement from the University of Cambridge and celebrate her 70th birthday.

Wednesday 13th December 2017 10.00–18.00

Department of Zoology and
University Museum of Zoology,
Downing Street, Cambridge, CB2 3EJ.

The conference will present new research by Jenny's colleagues, collaborators and former students on many of the topics that she has explored during her remarkable career.

The conference is free
but **please register** by 17th November 2017 by emailing Tim Smithson at ts556@cam.ac.uk

We hope you will join us
Per Ahlberg, Marcello Ruta, Tim Smithson.

The Palaeontological Association

Reg. Charity No. 1168330

The Palaeontological Association (PalAss) is a charity that promotes the study of palaeontology and its allied sciences through publications, sponsorship of meetings and workshops, provision of web resources and a large annual programme of awards and grants.

Membership is open to all for £30 per year, with reduced subscriptions for students and retired members at just £15 a year. In return, members receive the Association's newsletter, online access to the PalAss journals *Palaeontology* and *Papers in Palaeontology* and discounts on Field Guides and other publications. Members are also eligible for Association awards and grant schemes; for students this includes the Postgraduate Travel Fund.

The PalAss journals are high quality publications and we welcome new submissions. *Palaeontology* is now leading its field in publishing science that shapes and directs future research, while *Papers in Palaeontology* publishes high-quality taxonomic research set in context. Both journals offer a range of publishing options including open access, and we have a dedicated Publications Officer guiding the publication process.

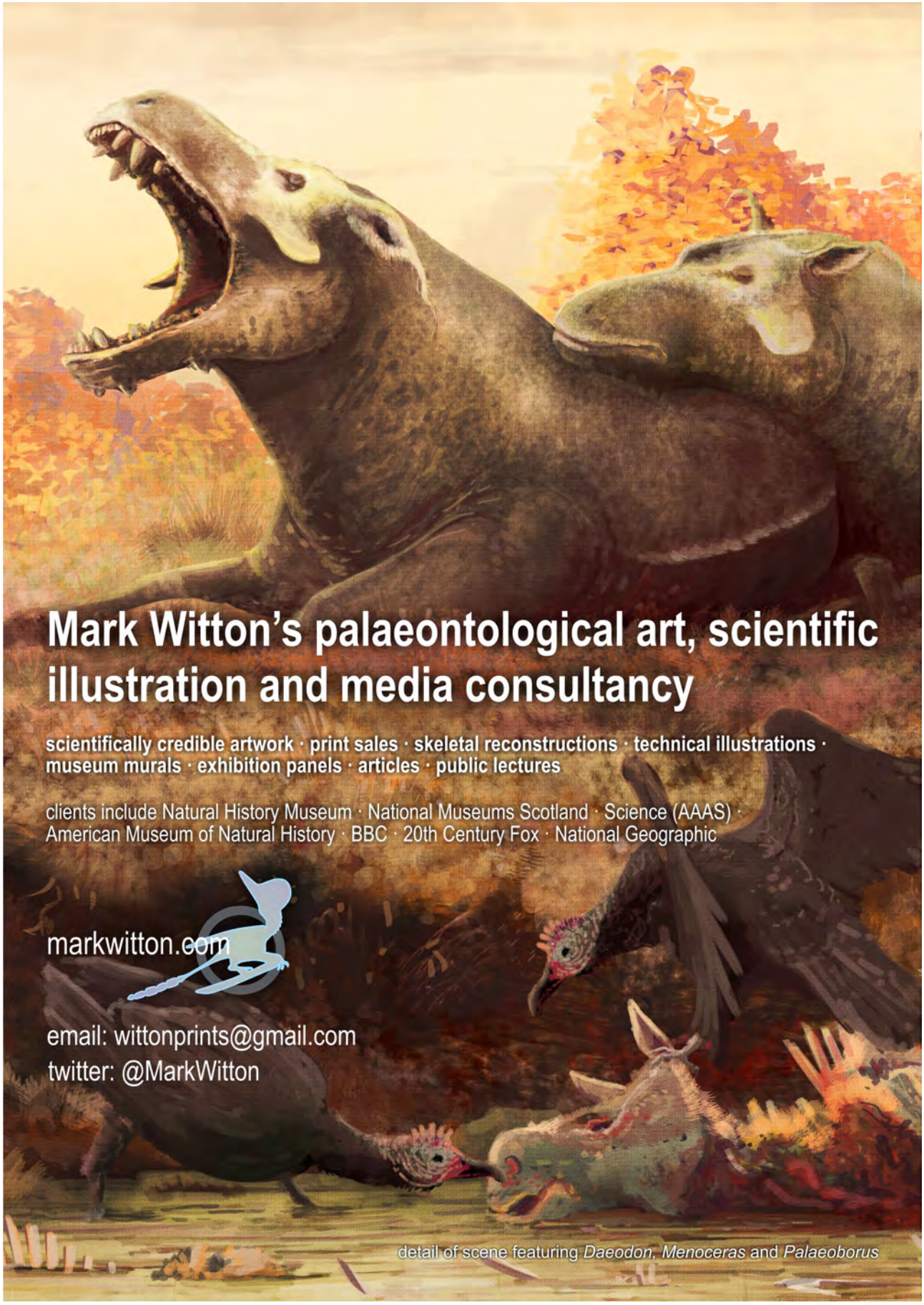
Our flagship Annual Meeting is a major international conference in December. Registration is subsidised for members, and contributions to travel costs are made to a large percentage of student members who are presenting their work. The President's Prize and Council Poster Prize are awarded to the best presentations from early career researchers each year with a cash prize and chance for an additional presentation. Achievement medals recognise notable contributions to our field.

The Association has a public engagement group that involves member volunteers (mainly postgraduate students) at outreach events around the UK. However, PalAss has members all over the globe and we welcome new members at www.palass.org. You can also find us on Facebook and Twitter (@ThePalAss).

Dr Jo Hellawell

Executive Officer
The Palaeontological Association

E-mail: **palass@palass.org**
Visit our website at: **www.palass.org**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detail of scene featuring *Daeodon*, *Menoceras* and *Palaeoborus*

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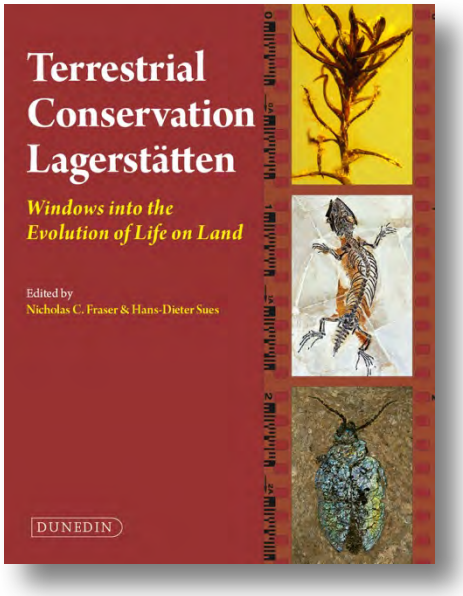
DUNEDIN

TO BE PUBLISHED SEPTEMBER 2017

Terrestrial Conservation Lagerstätten: Windows into the Evolution of Life on Land

15% discount offer*



Evolutionary biologists have long been concerned by the incompleteness of the fossil record. Although our knowledge of the diversity of life in 'deep time' has improved, many lineages of extant animals and plants still have only sparse fossil documentation. Even groups with 'hard parts' that render them suitable for fossilization often only have a limited record. Thus, although the fossil record is viewed as critical to the reconstruction of the evolutionary history of life, many biologists question its utility.

Fortunately discoveries of occurrences of exceptionally preserved fossils, known as conservation *Lagerstätten* (*Konservat-Lagerstätten*), shed much light on the past diversity of life. This volume reviews selected conservation *Lagerstätten* for terrestrial animals and plants throughout the Phanerozoic worldwide and includes sites in Asia, Europe and North and South America. Together the papers demonstrate the enormous progress made in recent years both in documenting the biodiversity of such extraordinary fossil deposits and also in elucidating the geological conditions for and biogeochemical processes behind the formation of conservation *Lagerstätten*.

Each contribution has been written by eminent palaeontologists who have enlisted additional ABSTexpertise to make each chapter as comprehensive as possible. The volume is edited by Nicholas C. Fraser of the National Museum of Scotland and Hans-Dieter Sues of the National Museum of Natural History of the Smithsonian Institution in Washington, DC.

Outline Contents: Introduction to conservation *Lagerstätten*; 1. Rhynie Chert (Early Devonian, Scotland); 2. East Kirkton (Early Carboniferous, Scotland); 3. Madygen Formation (Middle or Late Triassic, Kyrgyzstan); 4. Solite Quarry (Late Triassic, USA); 5. Yanliao Biota (late Middle Jurassic to early Late Jurassic, China); 6. Jehol Group (Early Cretaceous, China); 7. Santana Formation (Early Cretaceous, Brazil); 8. Amber (Mesozoic-Cenozoic, worldwide); 9. Messel (Eocene, Germany).

References appear at the end of each chapters .There is a single Index to the volume.

Hardback: ISBN 9781780460147 Colour illus. c. 450pp (260 x 200) Published prices: £165/ €199.00/ US$230.00

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SCHEDULE OF EVENTS

*Indicates platform and poster presentations by students (eligible for consideration for presentation prizes).

TUESDAY 12TH SEPTEMBER

09:00–18:00 SPPC and SVPCA registration open (Avon Lounge)

09:30–12:30 Workshops (Earth Sciences)

SESSION 1: SPPC
Avon Room (chair – Cindy Howells)

09:20–09:30 SPPC welcome and opening remarks

09:30–09:45 **Kieran Miles** - PROJECT AIRLESS: ADDRESSING THE PROBLEM OF PYRITE OXIDATION IN A LARGE FOSSIL COLLECTION

09:45–10:00 **Nigel Larkin & Steven Dey** - REPLICATING THE 1.8M LONG SKULL OF *PLIOSAURUS CARPENTERI* FOR DISPLAY

10:00–10:15 **Mark Graham** - THE REMEDIAL CONSERVATION AND SUPPORT JACKETING OF THE NEOTYPE OF THE DINOSAUR *MASSOSPONDYLUS CARINATUS*

10:15–10:30 **Donald Henderson** - FINDING AND COLLECTING A DINOSAUR IN AN OPEN PIT MINE – THE FORT MCMURRAY NODOSAUR

10:30–10:45 **Tim Ziegler** - BLOOD, SWEAT, AND VINEGAR: ACETIC ACID PREPARATION OF CETACEAN FOSSILS YIELDS EXCEPTIONAL RESULTS

10:45–11:15 Coffee (Avon Lounge)

11.15–12:45 Tours of the Lapworth Museum exhibition, store and archive

12:45–13:45 Lunch

SESSION 2: SYMPOSIUM – 'MACROEVOLUTION AND THE VERTEBRATE FOSSIL RECORD'
Avon Room (chairs – Roger Close, Ivan Sansom)

13:45–14:00 SVPCA welcome and opening remarks

14:00–14:30 **Anjali Goswami** - THE MACROEVOLUTIONARY CONSEQUENCES OF PHENOTYPIC INTEGRATION: FROM DEVELOPMENT TO

DEEP TIME

14:30–15:00	**Tom Kemp** - ANAGENESIS: THE NEGLECTED HALF OF MACROEVOLUTION
15:00–15:30	**Daniel Field** - MACROEVOLUTIONARY PATTERNS IN AVIALAE: BIRDWATCHING THROUGH GEOLOGICAL TIME
15:30–16:00	Coffee (Avon Lounge)
16:00–16:30	**Lauren Sallan** - MASS EXTINCTION, RECOVERY, AND THE ASSEMBLY OF BIODIVERSITY IN FISHES
16:30–17:00	**Catalina Pimiento *et al.*** - THE PLIOCENE MARINE MEGAFAUNA EXTINCTION AND ITS IMPACT ON FUNCTIONAL DIVERSITY
17:00–17:30	**Graeme Lloyd** - JOURNEYING THROUGH DISCRETE CHARACTER MORPHOSPACES: SYNTHESISING TEMPO, DISPARITY, AND PHYLOGENY
17:30–18:00	**Jason Head** - THE FUTURE OF THE PAST: INTEGRATING FOSSIL AND EXTANT ANATOMY WITH DEVELOPMENTAL DATA TO INFER VERTEBRATE MACROEVOLUTION
18:00–21:00	Icebreaker event, Lapworth Museum of Geology

WEDNESDAY 13TH SEPTEMBER

09:00–18:00 SPPC and SVPCA registration open (Avon Lounge)

SESSION 3
Avon Room (chair – Lauren Sallan)

9:15–9:30 **Joseph Keating *et al*.** - EARLY CAMBRIAN OSTRACODERMS AND THE TRIALS AND TRIBULATIONS OF TOTAL EVIDENCE DATING

9:30–9:45 ***Emma Randle & Robert Sansom** - A NOVEL PHYLOGENY FOR THE HETEROSTRACI: EVOLUTIONARY RELATIONSHIPS OF EXTINCT JAWLESS VERTEBRATES ON THE GNATHOSTOME STEM

9:45–10:00 **Zerina Johanson *et al*.** - FUSION IN THE VERTEBRAL COLUMN OF THE PACHYOSTEOMORPH ARTHRODIRE *DUNKLEOSTEUS TERRELLI* ('PLACODERMI')

10:00–10:15 **Plamen Andreev** - TOOTH-LIKE PATTERNING IN THE SCALES OF EARLY 'SHARKS'

10:15–10:30 ***Hermione Beckett *et al*.** - ADAPTIVE RADIATION OF PELAGIA (TELEOSTEI: ACANTHOMORPHA) INDICATED BY 3D MORPHOMETRY

10:30–11:00 Coffee (Avon Lounge)

SESSION 4
Avon Room (chair – Zerina Johanson)

11:00–11:15 **Francesco Santini** - TESTING ADAPTIVE RADIATION SCENARIOS IN MARINE FISHES BY COMBINING PHYLOGENOMIC AND PALEOBIOLOGICAL DATA

11:15–11:30 **Emily Rayfield *et al*.** - HOW DO MECHANICAL LOADS INFLUENCE CRANIAL SHAPE AND FUNCTION DURING DEVELOPMENT?

11:30–11:45 ***Struan Henderson *et al.*** - THE FIRST VIRTUAL CRANIAL ENDOCAST OF A POROLEPIFORM FISH AND THE EVOLUTION OF THE DIPNOMORPHA

11:45–12:00 **Jorge Mondéjar** - NEW ONYCHODONTID (OSTEICHTHYES; SARCOPTERYGII) REMAINS FROM THE MIDDLE DEVONIAN OF MOROCCO

12:00–12:15 **Jennifer Clack *et al*.** - NEW LATE DEVONIAN LUNGFISHES FROM GREENLAND MORPHOLOGICALLY AND PHYLOGENETICALLY BLUR THE D-C BOUNDARY

12:15–12:30 **Tom Challands *et al*.** - A CASE OF MISTAKEN IDENTITY: '*LATVIUS*' *OBRUTUS* AND NEW DIPNOANS FROM THE FRASNIAN

OF STOLBOVO, RUSSIA

12:30–13:45 Lunch

SESSION 5
Avon Room (chair – Stephan Lautenschlager)

13:45–14:00 **Neil Brocklehurst & Jörg Fröbisch** - A RE-EXAMINATION OF *MILOSAURUS MCCORDI*, AND THE EVOLUTION OF LARGE BODY SIZE IN CARBONIFEROUS SYNAPSIDS

14:00–14:15 ***David Ford & Roger Benson** - A RE-EXAMINATION OF *OROVENATOR MAYORUM* USING μCT DATA, AND ITS CONSEQUENCES FOR EARLY AMNIOTE PHYLOGENY

14:15–14:30 ***Davide Foffa *et al*.** - ECOMORPHOLOGICAL DISPARITY AND EVOLUTION OF MARINE REPTILES OF THE SUB-BOREAL JURASSIC SEAWAY

14:30–14:45 ***Susana Gutarra Diaz *et al*.** - USING COMPUTATIONAL FLUID DYNAMICS TO ANALYSE THE HYDRODYNAMIC PROPERTIES OF FOSSIL MARINE REPTILES

14:45–15:00 ***Pernille Venø Troelsen & Peter Falkingham** - RANGE OF MOTION AND HYDRODYNAMIC IMPLICATIONS OF THE LONG-NECK IN PLESIOSAURS

15:00–15:15 ***Catherine Klein *et al*.** - OPPORTUNITIES IN DISASTERS: MOLECULAR EVIDENCE FOR THE RAPID RADIATION OF SNAKES FOLLOWING THE CRETACEOUS-PALEOGENE MASS EXTINCTION

15:15–15:30 **Hugo Dutel *et al.*** - COMPARATIVE SKULL BIOMECHANICS IN *VARANUS* AND *SALVATOR* '*TUPINAMBIS*'

Lightning talks

15:30–15:50 ***Carla Bardua *et al.*** - MORPHOLOGICAL EVOLUTION OF THE CAECILIAN SKULL

Mark Evans *et al.* - THE SKULL OF THE MIDDLE JURASSIC PLESIOSAURIAN *CRYPTOCLIDUS* REVISITED

16:00–18:00 Poster session (Avon Lounge)
20:00–23:00 Annual auction (Old Joint Stock, city centre)

THURSDAY 14TH SEPTEMBER

09:00–14:00 SPPC and SVPCA registration open (Avon Lounge)

SESSION 6
Avon Room (chair – Emily Rayfield)

09:15–09:30 **Jeff Liston & Anthony Maltese** - HIPS, TIPS AND SWEET SWEPTBACK RAYS: LOOKING BEYOND TRADITIONAL CRANIAL CHARACTERS IN PACHYCORMIFORMES

09:30–09.45 ***Elizabeth Martin-Silverstone** - PTEROSAUR WING BONE GEOMETRY AND ITS RELATIONSHIP TO PNEUMATICITY AND PALAEOECOLOGY

09:45–10:00 **Mark Witton *et al*.** - GLIDE ANALYSIS AND BONE STRENGTH TESTS INDICATE POWERED FLIGHT CAPABILITIES IN HATCHLING PTEROSAURS

10:00–10:15 **David Unwin** - THE COMPLICATED AND SURPRISINGLY EARLY ORIGIN OF THE PTERODACTYLOID BAUPLAN

10:15–10:30 **Paul Barrett *et al.*** - UPPER KAROO VERTEBRATE ASSEMBLAGES (LATE TRIASSIC/EARLY JURASSIC) OF THE LATE KARIBA REGION, ZIMBABWE

10:30–11:00 Coffee (Avon Lounge)

SESSION 7
Avon Room (chair – Paul Barrett)

11:00–11:15 **Nicholas Longrich** - HIGH DIVERSITY OF SMALL DINOSAURS PRECEDING THE CRETACEOUS-PALEOGENE (K-PG) MASS EXTINCTION

11:15–11:30 ***Alfio Alessandro Chiarenza *et al*.** - THE EFFECT OF SPATIAL FOSSIL BIAS ON DINOSAUR PALAEODIVERSITY ESTIMATES IN THE LATEST CRETACEOUS OF NORTH AMERICA

11:30–11:45 **Donald Henderson *et al*.** - THE FORT MCMURRAY NODOSAUR – A THREE-DIMENSIONAL DINOSAUR FOSSIL WITH PRESERVED SCALES, PIGMENTS, AND STOMACH CONTENTS

11:45–12:00 **Karl Bates & Peter Falkingham** - PHILOSOPHICAL PERSPECTIVES ON BIOMECHANICAL RECONSTRUCTIONS OF EXTINCT ANIMALS: A CASE STUDY USING *TYRANNOSAURUS REX*

12:00–12:15 ***Robert Brocklehurst *et al*.** - MAKING MORPHOLOGY MOVE: XROMM VENTILATION KINEMATICS OF EXTANT ARCHOSAURS AND RECONSTRUCTING RIB MOTION IN FOSSILS

12:15–12:30 ***Ryan Marek *et al*.** - GRABBING EVOLUTION BY THE THROAT: FUNCTIONAL REGIONALISATION OF THE AVIAN CERVICAL COLUMN

Lightning talks

12:30–12:40 ***Femke Holwerda & Jeff Liston -** AN ANTERIOR SAUROPOD CAUDAL FROM THE PETERBOROUGH OXFORD CLAY: WHOSE TAIL IS IT ANYWAY?

Hebert Bruno Nascimento Campos *et al. - A UNIQUE EXCEPTIONALLY WELL-PRESERVED PTEROSAUR SKULL FROM THE CRATO FORMATION OF BRAZIL

12:45–14:00 Lunch

SESSION 8
Avon Room (chair – Susannah Maidment)

14:00–14:15 **Philip Mannion *et al*.** - SPATIOTEMPORAL PATTERNS IN FOSSIL SAMPLING BIAS AND THEIR IMPACT ON UNDERSTANDING THE EVOLUTIONARY HISTORY OF TERRESTRIAL CROCODYLOMORPHS

14:15–14:30 ***Pedro Godoy *et al*.** - EVOLUTION OF BODY SIZE IN CROCODYLOMORPHA IN A MULTI-REGIME EVOLUTIONARY LANDSCAPE

14:30–14:45 **Roland Sookias** - IMPROVING MORPHOLOGICAL CHARACTER CHOICE IN PHYLOGENETIC INFERENCE - DATA FROM MODERN CROCODILIANS

14:45–15:00 **Robert Sansom & Matthew Wills** - DIFFERENCES BETWEEN HARD AND SOFT DATA IN PHYLOGENETIC ANALYSES

15:00–15:15 ***Aime Rankin & Robert Asher** - MORPHOLOGICAL DATA PARTITIONING AND PHYLOGENETIC SIGNAL IN RODENTS

15:15–15:30 **Stephan Lautenschlager** - THE ROLE OF MINIATURISATION FOR CRANIAL FUNCTION ACROSS THE CYNODONT-MAMMALIAFORM TRANSITION

15:30–15:45 ***Elsa Panciroli *et al.*** - THE DENTARY OF *WAREOLESTES REX* AND NEW FOSSIL MAMMAL MATERIAL FROM THE MIDDLE JURASSIC OF SKYE, SCOTLAND

15:45–16:15 Coffee (Avon Lounge)

SESSION 8
Avon Room (chair – Phil Cox)

16:15–16:30	***Gemma Benevento *et al*.** - NEW DATA ON *MOERITHERIUM* FROM THE BIRKET QARUN FORMATION (EOCENE), FAYUM DEPRESSION, EGYPT
16:30–16:45	**Robert Asher** - TEETH, DEVELOPMENT, AND HYRAXES
16:45–17:00	**Charlotte Brassey** - THE FUNCTIONAL MORPHOLOGY OF THE CARNIVORAN BACULUM
17:00–17:15	**Elizabeth Kerr *et al*.** - THE RECENT NOW: POST-MEDIEVAL WOOD MICE
17:15–17:30	***Philip Morris *et al*.** - THE BIOMECHANICAL SIGNIFICANCE OF THE RODENT MANDIBULAR INCISOR “ROOT” - A FINITE ELEMENT ANALYSIS STUDY
17:30–17:45	***Thomas O’Mahoney *et al*.** - A VIRTUAL RECONSTRUCTION AND VOLUMETRIC MASS ESTIMATE OF AL288-1, *AUSTRALOPITHECUS AFARENSIS*
20:00–23:00	Annual dinner (Celebrity Indian Restaurant, city centre)

LIST OF POSTER PRESENTATIONS

Eduardo Ascarrunz & Walter Joyce - A REVISION OF THE MORPHOLOGY AND SYSTEMATICS OF GEOEMYDIDS (TESTUDINES: CRYPTODIRA) FROM THE MESSEL PIT QUARRY

Juan Benito *et al*. - QUANTIFYING THE QUALITY OF THE MESOZOIC MARINE TETRAPOD FOSSIL RECORD

***Emily Brown *et al*.** - QUANTIFYING THE COMPLETENESS OF THE BAT FOSSIL RECORD

***Leah Callender-Crowe & Robert Sansom** - EVALUATING THE PERFORMANCE OF MORPHOLOGICAL PARTITIONS IN RECOVERING AVIAN EVOLUTIONARY HISTORY

***Amy Campbell** - THE ANATOMY AND RELATIONSHIPS OF *EUCAMEROTUS FOXI* (DINOSAURIA, SAUROPODA) FROM THE EARLY CRETACEOUS OF ENGLAND

***Daniel Cashmore *et al*.** - CHARACTER COMPLETENESS OF TEMNOSPONDYL AMPHIBIANS: A NEW METHOD TO ASSESS OUR KNOWLEDGE OF CHARACTER CHANGES THROUGH TIME

Roger Close *et al*. - PATTERNS OF ALPHA DIVERSITY FOR PHANEROZOIC TERRESTRIAL VERTEBRATES

***Sally Collins *et al*.** - TOOTH DAMAGE, LOSS AND REPLACEMENT IN PYCNODONT FISHES

Lene Delsett *et al*. - NEW DATA ON THE OPHTHALMOSAURID BASICRANIUM

***Paige dePolo *et al*.** - *DELTAPODUS* FOOTPRINTS PROVIDE EVIDENCE OF STEGOSAURS ON ISLE OF SKYE (SCOTLAND, UK) IN THE MIDDLE JURASSIC

***Emma Dunne *et al*.** - TERRESTRIAL TETRAPOD DIVERSITY & BIOGEOGRAPHY ACROSS THE CARBONIFEROUS/PERMIAN BOUNDARY

Madeleine Geiger & Robert Asher - CORRELATES OF MAMMALIAN TOOTH ERUPTION PATTERNS

Josh Hedge *et al*. – AN ICHNOLOGICAL STUDY OF THE SALOP FORMATION (UPPER CARBONIFEROUS) OF SHROPSHIRE

***Ally Irwin** - PALAEOPATHOLOGICAL TRENDS IN JURASSIC MARINE REPTILES

Kotaro Ishikawa & Tomohiko Hori - IDENTIFICATION OF SMALL CARNIVORE FOSSILS USING BRAIN ENDOCASTS

***Andrew Jones & Richard Butler** - RESOLVING PHYTOSAURIA: A TRIFOLD CLADISTIC APPROACH

Nigel Larkin & Steven Dey - RECORDING THE UNCOLLECTABLE WITH LOW COST

LOW TECH: SUCCESSFUL PHOTOGRAMMETRY IN THE FIELD USING A MOBILE PHONE TO CREATE DIGITAL 3D MODELS

***Sophie Macaulay *et al*.** - A QUANTITATIVE EVALUATION OF PHYSICAL AND DIGITAL APPROACHES TO CENTRE OF MASS ESTIMATION

Martin Munt *et al*. - NEW SPINOSAURID DINOSAUR FINDS FROM THE WESSEX FORMATION (WEALDEN GROUP, EARLY CRETACEOUS) OF THE ISLE OF WIGHT

Darren Naish - REVIEWING THE VERTEBRATE FOSSIL RECORD

Attila Ősi & Jonatán Rudolf - SYSTEMATICS OF LATE CRETACEOUS EUROPEAN ANKYLOSAURS: THE IMPORTANCE OF THE DERMAL ARMOUR

Spyridoula Pappa *et al*. - ELEPHANT DUNG, CHEWED ANTLERS, WEATHERED BONES: DOCUMENTING A UNIQUE TAPHONOMIC COLLECTION

Stuart Pond - THE MOST COMPLETE ANKYLOSAUR SKULL EVER FOUND IN THE WESSEX SUB-BASIN (LOWER CRETACEOUS) OF THE ISLE OF WIGHT

***Jonathan Rio & Philip Mannion** - APPLYING THE FOSSIL RECORD OF CROCODYLIA TO ASSESS EXTINCTION RISK TODAY

Aubrey Jane Roberts *et al*. - THE EARLY TRIASSIC BONE BEDS OF SPITSBERGEN – MARINE ECOSYSTEM RECOVERY AFTER THE P/T EXTINCTION EVENT

***Christina Shears-Ozeki** - BORED BONES FROM THE TERRESTRIAL MIDDLE CRETACEOUS KEM-KEM BEDS OF SOUTHEAST MOROCCO

Timothy R. Smithson *et al*. - A NEW MISSISSIPPIAN TETRAPOD FROM FIFE, SCOTLAND, AND ITS ENVIRONMENTAL CONTEXT

***Max Stockdale & Michael Benton** - TEMPERATURE AND VARIABLE RATES OF CROCODYLOMORPH BODY SIZE EVOLUTION

Ikuko Tanaka *et al*. - VARIABILITY OF THE FOOTPRINTS OF ORIENTAL STORK (*CICONIA BOYCIANA*; AVES, CICONIIDAE) IN HOMOGENEOUS SEDIMENT

Mike Taylor & Matt Wedel - A UNIQUE MORRISON-FORMATION SAUROPOD SPECIMEN WITH BICONCAVE DORSAL VERTEBRAE

Mathew Wedel *et al*. - GROWTH SERIES OF ONE: CASE STUDIES IN TIME-TRANSGRESSIVE MORPHOLOGY

SPPC TALK ABSTRACTS

THE REMEDIAL CONSERVATION AND SUPPORT JACKETING OF THE NEOTYPE SPECIMEN OF THE DINOSAUR *MASSOSPONDYLUS CARINATUS*

Mark R. Graham

The Conservation Centre, Core Research Laboratories, Natural History Museum, London, UK

In March 2017 the neotype specimen of the Early Jurassic South African prosauropod dinosaur *Massospondylus carinatus* was appraised and condition reported at the Evolutionary Studies Institute, University of the Witwatersrand (WITS), Johannesburg, in readiness for remedial conservation and re-storage. The work was necessitated by deterioration of the specimen, which was caused by handling over a number of years and an inadequate and failing support mount.

Formally numbered BP/1/4934, but more affectionately known to staff as 'Big Momma', the specimen was contained within several individual blocks on flimsy support bases and presented various conservation challenges. These included treatment of fractures and cracking across several surfaces of the fossil and the production of clam shell supports to allow for articulated display within the constraints of an existing display cabinet. Part of the brief was to facilitate safer handling and access for researchers.

This project was led by the author who also trained the curatorial and preparation staff at WITS in the methods and techniques employed. The visit was funded by the Palaeontological Scientific Trust (PAST), the DST/NRF Centre of Excellence in Palaeosciences and The University of the Witwatersrand (WITS).

FINDING AND COLLECTING A DINOSAUR IN AN OPEN PIT MINE – THE FORT MCMURRAY NODOSAUR

Donald Henderson

Royal Tyrrell Museum of Palaeontology, Canada

In 2011 a shovel operator working in the Suncor Millennium Mine in northern Alberta bumped into an exceptionally preserved armoured dinosaur contained in a single, very large concretion. The force of impact of the bucket knocked many pieces off the concretion, resulting in a period of 2 days of searching by hand through rubble for small pieces before collection of the remaining fossil could begin. The position of the remainder, located 8 m up in a vertical cliff, required the use of a variety of heavy equipment to expose the specimen before it could be collected. After partly exposing the concretion, a high-pressure water and vacuum system was used to remove the last of the softer matrix, and to undercut the concretion. The rapid development of the concretion around the carcass soon after the animal's death, prevented the fossil from becoming permineralized. This unexpected lack of mechanical strength of the specimen, due to the very soft nature of the skeleton and armour, led to the collapse of the concretion into multiple pieces when it was lifted. The remaining pieces were then collected by stabilizing exposed surfaces with

a penetrant stabilizer, and then using standard burlap and plaster jackets. Some of the larger, fractured pieces were held together with various webbing and ratchet-straps prior to jacketing. An 800 km return trip by road to the Museum required novel packing and stabilizing methods to avoid abrasion and vibration problems.

REPLICATING THE 1.8M LONG SKULL OF *PLIOSAURUS CARPENTERI* FOR DISPLAY

Nigel Larkin[1] & Steven Dey[2]

[1]*Cambridge University Museum of Zoology, UK*
[2]*ThinkSee3D Ltd, Eynsham, UK*

The type specimen of *Pliosaurus carpenteri* from Westbury in Wiltshire is the most complete skeleton of its genus known, with an estimated body length of 8 m. The whole skeleton was mounted for display at Bristol City Museum & Art Gallery in 2017 for the first time since its excavation in 1994. However, the skull is 1.8 m long, very heavy and consists of sixteen fragile pieces. Mounting the real skull in position would have required a large amount of unsightly supporting metalwork that would have obscured some very interesting pathology on the palate.

One option was to CT-scan the skull pieces and mount 3D prints of the subsequent digital models. This would present less risk to the specimen than traditional moulding and casting and could possibly be quicker and cheaper. Importantly, the process would also provide 3D morphological data of the skull's internal anatomy for research for the first time. But would the resulting replica look real or horribly fake? After CT scanning the skull pieces, replicas were 3D-printed in gypsum and acrylic using a powder based 3D printer. After mounting these pieces together with internal metalwork, the replica was coloured with artists' acrylic paints to match the fossil. Casts of the teeth were adhered in position, which would have been problematic if the real skull had been used.

Satisfyingly, at the opening of the exhibition many well-known palaeontologists viewing the specimen failed to recognise that the skull they were looking at was in fact a replica. It passed.

PROJECT AIRLESS: ADDRESSING THE PROBLEM OF PYRITE OXIDATION IN A LARGE FOSSIL COLLECTION

Kieran Miles

Natural History Museum, London, UK

The Natural History Museum in London holds around 7 million fossils, a diverse collection of huge scientific and historical importance. The Conservation Centre is responsible for a wide range of specimen care issues, including those affecting the palaeontology collections. One of the most serious of these problems is pyrite oxidation. Pyrite, a form of iron sulphide, can often be found in fossils or their surrounding matrix. Oxidation occurs when unstable pyrite, often in its microcrystalline form, reacts with atmospheric oxygen and water. This reaction is accelerated at relative humidity above 60%, and produces a variety of harmful by-products, usually comprising ferrous sulphate, hydrogen sulphide and

sulphuric acid.

Airless, a three-year project that started in August 2015, aims to address this problem. The goal is to identify, treat and prevent pyrite oxidation in the Earth Science collections. A small team of conservation technicians are surveying the collections looking for signs of pyrite decay. Affected specimens are taken to a dedicated lab space where remedial treatments, such as dry brushing or ammonia vapour treatment, are carried out, before re-storage of specimens in anoxic microenvironments. These are individually hand-made using barrier film, with oxygen scavenging sachets added to remove oxygen from the sealed bag. In addition, the project has a digitisation aspect, with the use of web-based applications, improving the museum's database with high-quality photographs that partly compensate for the reduced physical access to the specimens. To date, the team has completed work on nearly 3000 specimens, including ichthyosaurs, plesiosaurs and pterosaurs.

BLOOD, SWEAT, AND VINEGAR: ACETIC ACID PREPARATION OF CETACEAN FOSSILS YIELDS EXCEPTIONAL RESULTS

Tim Ziegler[1], Erich M.G. Fitzgerald[2], James L. Goedert[3] & Matthew R. McCurry[2]

[1]*Geosciences, Museum Victoria, Melbourne, Australia*
[2]*National Museum of Natural History, Smithsonian Institution, Washington, DC, USA*
[3]*Burke Museum of Natural History and Culture, University of Washington, Seattle, Washington, USA*
[4]*Monash Biomedicine Discovery Institute and Centre for Human Anatomy Education, Department of Anatomy and Developmental Biology, Monash University, Melbourne, Australia*

Apprehensions about long preparation time, cost of consumables and even personal safety often cause researchers and institutions to eschew the use of acid to prepare fossils in favour of a mechanical approach. Indeed, inconsistently applied chemical preparation protocols can rapidly permit irreversible fossil corrosion. This is seen as particularly pertinent in the preparation of cetacean fossils, which are vulnerable due to their large size, thin neocortex and abundant trabecular bone. We show these factors are mitigable by a methodology employing briefer acid immersions, longer neutralisation times and systematic consolidation and protection of exposed bone. Museums Victoria has accelerated a technical programme preparing Cenozoic marine tetrapods including cetaceans, pinnipeds and birds, following prior institutional advances in the preparation of three-dimensionally preserved Devonian placoderms and Cretaceous mammal microfossils. As an example, we present the cranium and tympanoperiotics of an allodelphinid odontocete, cf. *Arktocara* (NMV P252767), collected in a calcareous concretion by James L. Goedert from the Upper Oligocene Lincoln Creek Formation (Grays Harbor County, Washington, USA). Cetacean fossils from the North Pacific are notoriously difficult to prepare, due to bioerosion by siboglinid *Osedax* worms and subsequent tectonisation of sediments along the Pacific active margin. This specimen was prepared primarily with acetic acid over 13 months, with exceptional anatomical detail retained to a degree not achievable mechanically or by less-stringent acid protocols. This is shown by comparisons with examples of previously prepared North Pacific cetacean fossils, and of acid corrosion on an Australian Cretaceous ichthyosaur, Miocene marsupial megafauna, and an in-preparation Miocene odontocete.

SVPCA SYMPOSIUM ABSTRACTS

MACROEVOLUTIONARY PATTERNS IN AVIALAE: BIRDWATCHING THROUGH GEOLOGICAL TIME

Daniel Field

University of Bath, UK

Birds are among the most diverse and ubiquitously distributed tetrapod clades; they inhabit a myriad of different environments, and exhibit incredible disparity in their forms and lifestyles. Unravelling how, when, and why this diversity has arisen demands an appeal to the fossil record of crown birds (Neornithes), as fossils provide us with the only direct evidence of neornithine evolutionary history. Additionally, understanding the origins of the features that make birds unique—such as feather-assisted flight—forces us to look outside of Neornithes to the avian stem lineage, where the nature, timing, and order of character transformations are only accessible through fossils. I will discuss recent macroevolutionary advances related to crown birds and their close relatives among non-avian dinosaurs, covering questions like “how did the ancestors of modern birds survive the end-Cretaceous mass extinction event that eliminated their stem-group relatives?”; “how and why have the biogeographic distributions of modern bird groups changed throughout their evolutionary history?”; and “just how ancient is modern avian powered flying potential?”.

THE MACROEVOLUTIONARY CONSEQUENCES OF PHENOTYPIC INTEGRATION: FROM DEVELOPMENT TO DEEP TIME

Anjali Goswami

University College London, UK

Phenotypic integration is a pervasive characteristic of organisms. Interactions among morphological traits, termed phenotypic integration, can be readily identified through quantitative analysis of geometric morphometric data from living and extinct organisms. These interactions have been hypothesized to be a fundamental influence on morphological evolution on small to large time scales. Simulations using covariance matrices derived from landmark data for diverse vertebrate taxa confirm that trait integration can influence the trajectory and magnitude of response to selection. At a macroevolutionary scale, phenotypic integration also produces both more and less disparate organisms than would be expected under random walk models, thereby increasing occupied morphospace range, but also homoplasy and convergence. However, this effect may not translate simply to evolutionary rates.

The role of integration in shaping morphological evolution is particularly interesting when combined with the observation from many studies that cranial integration changes through ontogeny and that postcranial integration is correlated with reproductive strategy in mammals. If integration directs morphological variation, functional pressures at various points in ontogeny may differ in consequence depending in part on level and pattern of integration. For example, high integration in early postnatal ontogeny in marsupials, combined with strong functional pressures for crawling and suckling, may have contributed

to the low variance observed in early postnatal marsupials and low disparity across marsupials, relative to placentals. Here, I discuss the macroevolutionary consequences of interactions among phenotypic integration, ontogeny, and function with comparative data from living and extinct vertebrates.

THE FUTURE OF THE PAST: INTEGRATING FOSSIL AND EXTANT ANATOMY WITH DEVELOPMENTAL DATA TO INFER VERTEBRATE MACROEVOLUTION

Jason Head

Department of Zoology and University Museum of Zoology, University of Cambridge, UK

Understanding vertebrate macroevolutionary transitions has traditionally been based primarily on comparative anatomy in a pattern-based school of inference during the 19th-mid 20th centuries. Discoveries of regulatory genetic functions and molecular mechanisms in patterning morphology have dominated vertebrate studies since, incorporating embryological data from a few model taxa in a predominately process-based school of inference. Despite this disjunct, pattern- and process-based approaches both are necessary for a sophisticated understanding of macroevolutionary history, as typified by studies of the evolution of snake-like body forms within squamates.

Evolutionary changes in expression of *Hox* genes that pattern discrete anatomical regions of the axial skeleton in other vertebrates have been proposed to result in an apparent deregionalization of the axial skeleton in snake-like body forms, including the losses of a distinct cervico-thoracic transition and a ribless lumbar region. These hypotheses are based on embryological comparisons of a single model snake taxon to *Mus* and a small sample of lizard taxa, and do not examine the distribution of *Hox*-regulated morphologies across Squamata as tests of process. Placing axial morphologies of extant and fossil squamates in a phylogenetic context does not support the hypothesis that loss of a ribless lumbar region occurred in the evolution of snakes, and quantifying vertebral morphology throughout Squamata reveals regional differences associated with *Hox* expression boundaries that were previously thought to be non-functional. Thus, integration of morphological and developmental data reveals the evolution of both regulatory gene function and phenotypic expression, as well as the necessity of fossils for understanding both.

ANAGENESIS: THE NEGLECTED HALF OF MACROEVOLUTION

Tom Kemp

University of Oxford

G. G. Simpson classically distinguished cladogenesis, referring to taxon branching, from anagenesis, relating to transformation of a single lineage. Modern systematic procedure of only recognising clades based on branch points reconstructed by apomorphy has resulted in almost all current work on macroevolution focussing on cladogenesis – the diversification of taxa over time and space. There are, however, equally valid questions about anagenesis at the macroevolutionary level.

How is the functional integration of the organism maintained even when changes in many

characters occur? The correlated progression model of small changes in functionally interconnected traits offers the best account.

What controls the direction of travel of a long lineage through morphospace? Tracking long-lasting, multi-dimensional gradients in a metaphorical adaptive landscape models the process, but do they exist?

Why have so few lineages evolved beyond a low taxonomic level to achieve the conventional status of a new order, class or phylum? Because there are only a few sufficiently complex, long lasting ecological gradients available, such as water to land, ectothermic to endothermic niches, etc.

How does major anagenetic transformation relate to cladogenetic branching? In terms of the adaptive landscape metaphor, as periodic plateaus along a flat-topped ridge.

Why is there so little current interest in this particular area of evolution? Is it due to the constraints imposed by cladistic methodology excluding anagenesis from systematics; to too little evidence to support hypotheses (pejoratively called “scenarios”); to the decline of anatomical, functional morphological, and physiological teaching in favour of molecular and quantitative biology?

JOURNEYING THROUGH DISCRETE CHARACTER MORPHOSPACES: SYNTHESISING TEMPO, DISPARITY, AND PHYLOGENY

Graeme Lloyd

School of Earth and Environment, University of Leeds, UK

The morphological complexity of the vertebrate skeleton offers a rich data set that can offset deficiencies in their fossil record. One form of encoding such data is the discrete character-taxon matrix that first came to prominence in the middle of the twentieth century and has been utilised to understand evolutionary tempo, morphological diversity, and phylogenetic inference. The synthesis of these three approaches can best be understood in the context of an ordination space where empirical observations are connected by the branches of a phylogenetic hypothesis (previously scaled to geologic time) and separated by morphologic distances. Constructing such spaces is complicated by, amongst other things, the non-Euclidean nature of morphologic distances, the prevalence of phylogenetic uncertainty, and difficulties associated with visualizing hyperdimensional spaces. In addition, the literature contains at least three different approaches for reconstructing hypothetical ancestors (internal nodes) with no clear comparison or preference established. Here I outline current approaches for generating discrete character “chronophylomorphospaces”, apply some new metrics to understand how choices related to ancestral reconstructions affect our understanding of evolutionary tempo and morphological diversity, and identify some outstanding problems and their potential solutions. I show that some ancestral reconstruction approaches can lead to ordination spaces based more on phylogenetic rather than morphologic distances and that the choice to reconstruct ancestors pre- or post-ordination can dramatically alter our perception of evolution. Finally, I show that, complementary to a range of other studies, an early burst of morphological evolution is a common feature of vertebrate data sets.

THE PLIOCENE MARINE MEGAFAUNA EXTINCTION AND ITS IMPACT ON FUNCTIONAL DIVERSITY

Catalina Pimiento[1,2,3], John Griffin[2], Christopher Clements[4], Daniele Silvestro[5], Sara Varela[1] Mark Uhen[6] & Carlos Jaramillo[3]

[1]*Museum für Naturkunde, Berlin, Germany*
[2]*Swansea University, UK*
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[4]*University of Zurich, Switzerland*
[5]*University of Gothenburg, Sweden*
[6]*George Mason University, USA*

The end of the Pliocene marked the beginning of a period of great climatic variability and sea-level oscillations. Here, based on a new analysis of the fossil record, we identify a previously unrecognized extinction event among marine megafauna (mammals, seabirds, turtles and sharks) during this time, with extinction rates three times higher than in the rest of the Cenozoic, and with 36% of Pliocene genera failing to survive into the Pleistocene. To gauge the potential consequences of this event for ecosystem functioning, we evaluate its impacts on functional diversity, focusing on the 86% of the megafauna genera that are associated with coastal habitats. Seven (14%) coastal functional entities (unique trait combinations) disappeared, along with 17% of functional richness (volume of the functional space). The origination of new genera during the Pleistocene created new functional entities and contributed to a functional shift of 21%, but minimally compensated for the functional space lost. Reconstructions show that from the late Pliocene onwards, the global area of the neritic zone significantly diminished and exhibited amplified fluctuations. We hypothesize that the abrupt loss of productive coastal habitats, potentially acting alongside oceanographic alterations, was a key extinction driver. The importance of area loss is supported by model analyses showing that animals with high energy requirements (homeotherms) were more susceptible to extinction. The extinction event we uncover here demonstrates that marine megafauna were more vulnerable to global environmental changes in the recent geological past than previously thought.

MASS EXTINCTION, RECOVERY, AND THE ASSEMBLY OF BIODIVERSITY IN FISHES

Lauren Sallan

University of Pennsylvania, USA

The term “Mass Extinction” brings to mind geologically-instantaneous devastation of the biosphere and global, thorough collapse of ecosystems, in which short-term survival determines the ultimate outcome. This view has been supported by previous work on the famous “Big Five” events, focused on marine invertebrates and on terrestrial tetrapods. Until recently, fishes were largely excluded from such studies due to a lack of appropriate databases, despite their importance in aquatic ecosystems, general diversity (>50% of vertebrate species) and extensive fossil record. Newly compiled databases for fossil fishes are upending our understanding of the role of global events in shaping vertebrate macroevolution. These have highlighted the selective nature of mass extinction, challenging the severity, scope and presumed causes of “Big Five” events. Indeed, second-order crises (e.g. end-Devonian, end-Jurassic) were likely more critical in shaping

the evolution and current biodiversity of aquatic vertebrates. Investigations of fish faunas and traits across extinction boundaries have shown that predictable ecological processes during prolonged recovery intervals (15–25 My) are just as, if not more, important as the triggering events in structuring subsequent biodiversity. Mere survival is not enough; long-term responses determine the ultimate outcome of global events. Quantitative investigation of the fish fossil record has, and will continue to, rewrite our understanding of both mass extinction and vertebrate macroevolution as a whole.

SVPCA LIGHTNING TALK ABSTRACTS

MORPHOLOGICAL EVOLUTION OF THE CAECILIAN SKULL

*Carla Bardua[1], David Gower[2], Mark Wilkinson[2], Emma Sherratt[3] & Anjali Goswami[1]

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[2]*Natural History Museum, London, UK*
[3]*University of Adelaide, Adelaide, Australia*

With just over 200 species, Gymnophiona are the smallest amphibian clade. Despite their generally similar appearances (e.g. limblessness), caecilians exhibit a broad range of skull morphologies. However, very few studies explore morphological evolution within this clade. We used geometric morphometrics to quantify cranial morphological variation across Gymnophiona and reconstruct evolutionary mode and rate across the clade. An intensive landmarking approach was used to capture the skull morphology of 34 caecilians, with representatives from every genus. Anatomical landmarks and sliding-semilandmarks were placed onto the skull of each specimen and an automated procedure in the R package "Morpho" was then used to place patch points onto the surface of each bone, positioning points to minimise bending energy of a Thin Plate Spline deformation. These landmark data were subjected to Procrustes analyses to remove non-shape aspects, followed by a series of analyses to reconstruct shape evolution and morphological rates through time in a phylogenetic framework. It was found that a kappa model of evolution best fitted these shape data (κ=0.38), suggesting moderately punctuated evolution. Skull morphology had a strong phylogenetic signal (K=0.80, $p=1\times10^{-4}$), showing that closely related species had similar morphologies. Allometry accounted for 17% of shape variation (R^2 =0.17, $p=1\times10^{-4}$). *Atretochoana eiselti* exhibited the fastest rate of morphological evolution, and represents the most extreme cranial morphology. One rate shift was found at the base of Scolecomorphidae, revealing fast morphological evolution in this family. This landmark approach allowed accurate representation of skulls across Gymnophiona and new insights into skull morphological evolution.

A UNIQUE EXCEPTIONALLY WELL-PRESERVED PTEROSAUR SKULL FROM THE CRATO FORMATION OF BRAZIL

*Hebert Bruno Nascimento Campos[1], Aude Cincotta[2], Eberhard Frey[1], Pascal Godefroit[3] & Johan Yans[2]

[1]*Staatliches Museum für Naturkunde Karlsruhe, Karlsruhe, Germany*
[2]*Department of Geology, University of Namur, Belgium*
[3]*Directorate 'Earth and History of Life', Royal Belgian Institute of Natural Sciences, Brussels, Belgium*

The posterior part of a skull from a tapejarid pterosaur was studied for the exceptional preservation of its soft-tissues. The specimen comes from the Early Cretaceous (Aptian) Crato Formation of northeastern Brazil. It shows a peculiar soft sagittal crest that gives new information about the anatomy and the diversity of tapejarids. The specimen lies on five limestone slabs. The bony part comprised the posterior part of the skull, with the braincase and one complex of three dorsally oriented and associated bony crests. The

crest consists of a huge and elongated parietal crest, a trabecular frontal crest, and an occipital spine. The specimen preserves the posterior parts of the nasoantorbital fenestra and orbit. The soft cranial crest is characterized by a multilinear dorsal crest with almost parallel fibres, which curve posteriorly. Pigment organelles – melanosomes – were observed in the crest as well as 'hair-like' fibres (pycnofibres). They present diverse shapes and sizes, suggesting diverse colorations for the soft tissues. The new tapejarid shares certain features with the tapejarids *Tupandactylus imperator* and "*Huaxiapterus*" *benxiensis*, which include an elongated parieto-occipital crest. Nonetheless, it differs from *Tupandactylus imperator* and *Ingridia navigans* by the following characteristics: absence of a suprapremaxillary spine, very dorsally oriented posterior crests, as well as a specific morphology for the soft crest. Our specimen can therefore be assigned to a new taxon of Tapejaridae, a group previously reported from the Crato Formation.

THE SKULL OF THE MIDDLE JURASSIC PLESIOSAURIAN *CRYPTOCLIDUS* REVISITED

Mark Evans[1,2], Roger Benson[3] & Stephanie Wright[3]

[1]*Leicester Arts and Museums Service, Leicester, UK*
[2]*Department of Geology, University of Leicester, UK*
[3]*Department of Earth Sciences, University of Oxford, UK*

The Callovian (Middle Jurassic) cryptoclidid *Cryptoclidus eurymerus* is one of the best-known plesiosaurians. Known from the Oxford Clay Formation of England, it has a character score of 95% in recent phylogenetic datasets.

A new specimen possesses an exceptionally complete, although dorsoventrally crushed, skull. The skull has been CT scanned, along with another previously described and similarly complete, but crushed, skull, allowing segmentation of individual bones. Our observations confirm previous descriptions of the jugal as a much-reduced splint of bone. Although the best example is still incomplete ventrally, the material suggests the lack of a tight osteological connection, thus rendering the region structurally weak.

Previous interpretation of the orbital margin regarded it as incompletely known due to abrasion. The new specimen demonstrates that the orbital margin is in fact poorly ossified, with many of the bones displaying a thin, crenelated or fluted edge. The orbital outline deviates from the expected suboval shape, with significant excavations posteromedially and posterolaterally. A robust and concave orbital margin, formed by the ascending process of the maxilla, is only present anteriorly and contributes only 10% to the total. This contrasts with the plesiomorphic condition (e.g. *Plesiosaurus*) in which the entire margin of the orbit is concave. Data from other cryptoclidids (e.g. 30% concave margin in *Muraenosaurus* sp.) suggest that a poorly ossified orbital margin is a synapomorphy of the clade and that transmission of stress between the maxillary dentition and dorsal skull roof would have been limited to the region anterior to the orbit.

AN ANTERIOR SAUROPOD CAUDAL FROM THE PETERBOROUGH OXFORD CLAY: WHOSE TAIL IS IT ANYWAY?

*Femke Holwerda & Jeff Liston

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The Callovian Oxford Clay of England has yielded a rich and diverse marine fauna, mainly discovered and described by Alfred Leeds. However, occasionally it also brought forth terrestrial fossils, including four isolated cases of sauropod remains, one of a stegosaurid, and another of a dryosaurid. Thus far, only *Cetiosaurus oxoniensis* and *Cetiosauriscus stewarti* are confirmed sauropod taxa from these beds.

Here, we describe an isolated sauropod anterior caudal vertebra from the Oxford Clay near Peterborough. Incomplete, it has been immersed in seawater post-mortem, indicated by the adhesion of molluscs, but some characters can nevertheless be used for diagnosis and comparisons.

The anterior articular surface is round, whereas the posterior articular surface is heart-shaped, as in many eusauropods, including *Cetiosaurus*. Interestingly, the ventral surface shows a keel-like structure; a character shared with neosauropods (e.g. *Barosaurus*) but also with an as yet unnamed Middle Jurassic sauropod caudal from York, UK.

The posterior side of the neural canal is teardrop-shaped, a character shared with most basal eusauropods. Below the posterior neural canal, a lip-like structure seems to be present; a character which is shared with *Cetiosaurus*. However, the anterior caudal transverse process (ACTP) complex is similar to, although more pronounced than *Cetiosauriscus*, being more similar to more derived sauropods (Neosauropoda).

Thus, an incomplete isolated element may help elucidate sauropod species diversity and dispersal in the Middle Jurassic of England.

SVPCA TALK ABSTRACTS

TOOTH-LIKE PATTERNING IN THE SCALES OF EARLY 'SHARKS'

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In chondrichthyans, odontodes are ubiquitous skeletal elements, components of dermal and oropharyngeal scales as well as the dentition. Despite years of intense study of odontode development from molecular, anatomical and evolutionary perspectives, there has not been a major breakthrough in understanding the origins of teeth and tooth patterning.

This study presents a new phylogenetic tree of jawed fish that puts at the base of the Chondrichthyes a plethora of mongolepid and other polyodontode scale species (e.g. *Tezakia*, *Canyonlepis*) that pre-date the first appearance of teeth in the Upper Silurian. Investigations of their scales via tomography, SEM and histological sections identify mechanisms of odontode addition/crown growth related to current theories of pattern formation in the skeleton of early fish.

Common for mongolepid scale crowns are linear rows of odontodes (odontocomplexes) remarkably similar in structure to the tooth whorls of 'acanthodians' and more conventional stem chondrichthyans such as *Doliodus*. These odontocomplexes are suggested to be capable of continuous orderly growth at one end by generation of ever larger elements in the absence of dental lamina. The dermal skeleton of chondrichthyans can thus be viewed to have primitively possessed the competence to organise odontodes in a manner characteristic of tooth families.

TEETH, DEVELOPMENT, AND HYRAXES

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The life history of animals includes aspects of growth and development such as attainment of maturity and gestation time. Such features are difficult to infer among fossils, but not impossible. I investigated dental homologies, development, and growth in living and fossil hyracoids and tested if hyracoids and other mammals show correlations between eruption patterns and aspects of life history. Most lower cheek teeth finish eruption during growth in hyracoids, not after growth as in most other afrotherians. All hyracoids show the m1 at (lower) or near (upper) the beginning of eruption of permanent teeth; m3 is the last permanent tooth to erupt. The living *P. capensis* erupts most lower antemolar loci before m2. In contrast, fossil hyraxes erupt lower antemolars after m2. The early eruption of antemolars correlates with increased gestation time and age at maturity in primates and *Tupaia* (i.e., ‘Schultz’s rule’), and modern hyraxes resemble some anthropoid primates in exhibiting long gestation and eruption of antemolars at or before molars. Among other afrotherians sampled so far, eruption patterns do not significantly covary with either life history parameter.

UPPER KAROO VERTEBRATE ASSEMBLAGES (LATE TRIASSIC/EARLY JURASSIC) OF THE LATE KARIBA REGION, ZIMBABWE

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Southern Africa provides critical information on Late Triassic–Early Jurassic terrestrial tetrapod faunas. Most of the localities in this region are in South Africa and Lesotho, but preliminary work in Zimbabwe has revealed significant potential. Early Jurassic Zimbabwean localities have yielded the basal sauropodomorph *Massospondylus*, the early sauropod *Vulcanodon* and theropod material. Late Triassic localities are also known, but have yielded only fragmentary specimens thus far.

In early 2017, a joint South African-Zimbabwean-UK team conducted fieldwork in the upper Karoo-aged deposits along the shores of Lake Kariba, northern Zimbabwe (Mid-Zambesi Basin). We relocated the *Vulcanodon* type locality on Island 126/127 and found that, contrary to previous reports suggesting a Toarcian age, the quarry was in a horizon pre-dating the onset of Drakensburg volcanism (= Batoka Basalts). It is situated instead within the earlier Lower Jurassic Forest Sandstone. This indicates that *Vulcanodon* is 10–15 million years older than thought previously, recalibrating several nodes within Sauropoda and indicating extensive overlap between true sauropods and 'prosauropods'.

Other new vertebrate localities show that sauropodomorphs are present in the Forest Sandstone and upper Tashinga (Late Triassic) formations, but a grey mudstone facies within the Pebbly Arkose Member of the latter unit yields a more aquatic fauna, including lungfish and phytosaurs, but lacking sauropodomorphs. The phytosaur occurrence is the first in Africa south of the Sahara. Faunal and sedimentological evidence indicates that the Late Triassic and Early Jurassic sites in this region were deposited under more mesic environments than their lateral equivalents in South Africa.

PHILOSOPHICAL PERSPECTIVES ON BIOMECHANICAL RECONSTRUCTIONS OF EXTINCT ANIMALS: A CASE STUDY USING *TYRANNOSAURUS REX*

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Bite performance predictions for *Tyrannosaurus rex* vary widely, despite recent modelling studies using near-identical methods. Here we examine previously proposed explanations for the disparity in estimates, in addition to presenting new analyses of model input data. We find no support for suggestions that the highly disparate estimates are the result of muscle volume reconstructions or specific assumptions of muscle contraction dynamics in earlier studies: in both instances standardising these parameters across studies increases,

rather than decreases, the difference in predicted bite force. New analyses of model inputs unambiguously indicate that the difference between studies results from subjective selection of muscle fibre lengths; longer fibre lengths in more recent studies result in smaller muscle cross sectional areas and subsequently lower muscle and bite force estimates. To examine this specific issue, and to guide future estimates of muscle fibre lengths in extinct animals more generally, we analysed the ratio of muscle fibre length (FL) to muscle length (ML) in over 1200 muscles of extant terrestrial vertebrates from various body regions. We find that FL:ML varies widely within and across body regions, but with strong convergence on a mean ratio of 0.45–0.55. Application of this ratio to *T. rex* jaw muscles results in higher-end muscle and bite forces favoured by earlier studies, though considerable uncertainty remains. Future work might constrain higher-end estimates through further analysis of jaw muscle architecture in living vertebrates and by incorporation of bone loading limits into computer simulations.

ADAPTIVE RADIATION OF PELAGIA (TELEOSTEI: ACANTHOMORPHA) INDICATED BY 3D MORPHOMETRY

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Pelagia (or Pelagaria) is an anatomically disparate clade of open-ocean fishes identified through molecular studies. It has been postulated that the ecologically distinct lineages of Pelagia diverged rapidly early in the group's history, perhaps shortly after the end-Cretaceous extinction. This differs from model 'adaptive radiations' like cichlid fishes and *Anolis* lizards in both age and geographic scale, but corresponds closely to the pattern for which the concept was first defined: Cenozoic mammals. We collected computed tomographic data for the crania of 56 extant species of Pelagia, sampling all 14 confirmed extant families and a quarter of living species. We use three-dimensional geometric morphometrics to generate a shape space for this sample of skulls. Cranial anatomy clearly separates families within Pelagia, paralleling conspicuous differences in body shape. Of note are the gempylids (snake mackerels) and trichiurids (scabbardfishes), which have elongate skulls, and the deep-sea chiasmodontids (black swallowers) with largely reduced opercular series, posteriorly directed suspensoria, and long gapes. We conducted a disparity-through-time analysis based on these shape data and existing molecular phylogenies to test for deviations from a Brownian motion model of phenotypic evolution. We find substantially lower-than-expected levels of subtree disparity early in the history of the clade, a pattern often interpreted as consistent with theoretical models of adaptive radiation. These results provide quantitative support for an adaptive radiation in Pelagia early in the Cenozoic. This morphometric framework will allow the inclusion of three-dimensionally preserved fossils of this group, allowing us to further constrain patterns of phenotypic diversification in Pelagia.

NEW DATA ON *MOERITHERIUM* FROM THE BIRKET QARUN FORMATION (EOCENE), FAYUM DEPRESSION, EGYPT

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Moeritherium is an early diverging proboscidean from the late Eocene–early Oligocene of Africa. Unlike other proboscideans, *Moeritherium* was characterised by a relatively small body size, a likely semiaquatic lifestyle, and is often reconstructed with either a small, tapir-like proboscis, or lacking one altogether. At least three species are currently recognised from isolated teeth, partial skulls and partial postcrania. Here we present new cranial and mandibular material of *Moeritherium* from the early Priabonian (~37 Ma) of Birket Qarun, Fayum Depression, Egypt, increasing our knowledge of its anatomy. These fossils include the oldest known cranial and mandibular material of *Moeritherium*. The skull appears distinct from previously described cranial material, but the teeth are morphologically similar to isolated teeth described from the broadly contemporaneous Bir El Ater locality, Algeria, suggesting an affinity with *M. chehbeurameuri*. We present the first digital reconstruction and analysis of the internal structures of the skull and mandible of *Moeritherium* based on µCT data for this specimen. From the cranium, a near complete three-dimensional model of the endocast was produced, permitting investigation of brain anatomy. Within the mandible, of particular interest is the large size of the mandibular canal, which extends labially to the tooth row, and occupies much of the internal space within the mandible. Among Paenungulata, sirenians share this feature with *Moeritherium*. Extant proboscideans, however, have smaller mandibular canals, more similar to hyraxes, indicating a complicated evolutionary—and perhaps functional—history of this feature.

THE FUNCTIONAL MORPHOLOGY OF THE CARNIVORAN BACULUM

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The mechanical behaviour of an individual's genitals directly impacts upon their fitness. If genitalia cannot function mechanically, the individual cannot deliver/receive sperm, and cannot produce viable offspring. Within carnivorans, males possess a mineralized element within the glans of the penis, which is extremely morphologically diverse. Baculum size and shape has previously been found to be under direct sexual selection. Yet the adaptive advantage of such a structure remains unclear.

I present a comparative analysis of modern carnivoran bacula with the aim of testing functional hypotheses, including their role in facilitating intromission, prolonging copulation duration and/or removal of competitors' sperm. 3D models of museum specimens (n=77, families=11) were generated from microCT. In the absence of numerous definitive homologous landmarks for GMM, alternative means of quantifying 'shape' are explored, including elliptical Fourier analysis, thickness mapping and curvature analysis. Biomechanical performance is derived from modified beam theory.

All shape metrics are found to contain a strong phylogenetic signal. Curvature does not

scale to body mass (r^2=0.01, p>0.05), and baculum 'relative strength' decreases in larger taxa (r^2=0.12, p=0.002). Baculum tip is more variable in shape than the shaft (t=4.97, p<0.001). Tip shape correlates to relative testes mass (a proxy for post-copulatory sexual selection; p=0.013, λ=-0.56), suggesting a role for the tip in biasing paternity via sperm competition or cryptic female choice.

Future research will quantify the rate of shape evolution in the tip versus base. Additionally, cadaveric material will be incorporated in order to consider the biomechanics of the whole soft tissue structure.

A RE-EXAMINATION OF *MILOSAURUS MCCORDI*, AND THE EVOLUTION OF LARGE BODY SIZE IN CARBONIFEROUS SYNAPSIDS

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Milosaurus mccordi was described in 1970 as a large pelycosaurian-grade synapsid from the late Carboniferous of Illinois, but has since received little attention. Here the holotype and referred material of *Milosaurus* is re-examined and incorporated into a recent phylogenetic analysis. *Milosaurus* is found to be the sister to Sphenacomorpha, sharing with this clade the posterodorsally expanded ischium and the calcaneum with a greater length than width, but the more plesiomorphic ischium indicates it is an outgroup to the clade rather than within it. Most of the referred material shows very little overlap with the holotype, and so most was not included in the cladistic analysis. However, what was originally described as a dorsal rib is judged to be a femur, sharing a highly distinctive morphology with the holotype.

With an estimated body mass of 41 kg, *Milosaurus* represents one of the largest Carboniferous synapsids. Large size evolved at least twice independently in Sphenacomorpha during the Pennsylvanian: once in Sphenacodontidae and once in Edaphosauridae. Using comparative phylogenetic methods, we re-examined body size evolution in sphenacomorphs with *Milosaurus* included. *Milosaurus* is found to represent an independent evolution of large size, but with its trait evolution considerably slower than was observed in the other sphenacomorph clades, indistinguishable from evolution under Brownian Motion. Nevertheless, as one of the earliest appearances of large body size in the amniote fossil record and the outgroup to the most diverse Paleozoic synapsid lineages, *Milosaurus* represents a crucial taxon for understanding early terrestrial ecosystems.

MAKING MORPHOLOGY MOVE: XROMM VENTILATION KINEMATICS OF EXTANT ARCHOSAURS AND RECONSTRUCTING RIB MOTION IN FOSSILS

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Modern birds have a highly efficient respiratory system, and a highly derived ribcage with which they ventilate their lungs via costosternal pumping. However, understanding the co-evolution of ribcage morphology and ventilation mechanics in birds has been hindered by a lack of integration between kinematic and anatomical data. In particular, birds differ significantly from their nearest living relatives, the crocodilians, in terms of their costovertebral anatomy. This makes it difficult to directly compare patterns of rib motion, which in turn prevents reconstruction of motion in fossil archosaurs. Here, we employ a joint-based approach to represent both bone morphology and motion. In vivo rib kinematics were recorded during ventilation in living crocodilians and birds using XROMM (X-ray reconstruction of moving morphology), with motion measured relative to the articular surfaces of the costovertebral joint; axes of rib translation and rotation were defined with respect to specific homologous landmarks on the ribs and vertebrae. This approach then served as the basis for “scientific motion transfer”, applying motion patterns observed in modern archosaurs to their fossil relatives - specifically, non-avian dinosaurs - in a framework grounded in the anatomy of the costovertebral joint. Whether to apply a rib motion pattern more similar to birds or crocodilians to dinosaurs was determined through detailed morphometric analysis of the vertebrae and ribs. This approach represents a testable and repeatable way of predicting ventilation kinematics in extinct taxa, and so should greatly improve our understanding of respiratory evolution along the avian stem.

A CASE OF MISTAKEN IDENTITY: ‘*LATVIUS’ OBRUTUS* AND NEW DIPNOANS FROM THE FRASNIAN OF STOLBOVO, RUSSIA

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The village of Stolbovo, western Russia, has previously yielded a dipnoan fauna comprising the long-snouted form '*Rhinodipterus' stolbovi*, but also a three-dimensionally preserved otoccipital region of a skull previously identified as the osteolepiform ‘*Latvius*’ *obrutus*. This identification was made from the density of lateral line canal pores in the skull roof bones in addition to what Vorobyeva (1977) described as the post-parietal, tabular and extratabular bones. Reexamination of this specimen does not recognise the osteolepiform dermal elements previously identified but rather a dipnoan configuration including a characteristic B-bone, lateral dermal elements and a dipnoan parasphenoid. MicroCT-scanning reveals an enlarged utricular recess in the vestibular system, the derived condition for lungfishes, and separate sacculae and lagenae also present in

rhinodipterid and dipterid dipnoans. Phylogenetic analysis resolves '*Latvius*' *obrutus* as the primitive sister taxon to the 'phaneropleurid-fleurantiid' clade – a clade comprising derived Middle–Upper Devonian lungfishes. '*Rhinodipterus' stolbovi* resolves among the more primitive griphognathids, typical Gondwanan forms, and is not a rhinodipterid. Additional isolated dipnoan skeletal elements from the site include tooth plates, parasphenoids, shoulder girdle elements and dermal elements and indicate at least an additional three lungfish taxa from Stolbovo. Of particular note is a ctenodiform tooth plate more characteristic of Carboniferous lungfishes. The new material and analyses not only demonstrate increased lungfish diversity from the Frasnian of Baltica but also probable interchange between Gondwana and Baltica during this time. Most importantly, Carboniferous-like forms appear more common in the Devonian than previously realised indicating that Carboniferous lungfishes likely represent a survival assemblage in addition to a new radiation of lungfish.

THE EFFECT OF SPATIAL FOSSIL BIAS ON DINOSAUR PALAEODIVERSITY ESTIMATES IN THE LATEST CRETACEOUS OF NORTH AMERICA

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Analyses of dinosaur diversity patterns through time have offered different interpretations when focusing on time intervals of important biotic events, such as the lead up to the K-Pg mass extinction. Although the general consensus suggests a sudden demise at the K-Pg boundary, others have proposed a gradual, long-term diversity decline. One of the main methodological obstacles is the estimation of the impact of spatial bias when reconstructing diversity, especially where sampling is minimal or absent. A possible solution is the application of ecological niche modelling, which uses species occurrences and climatic data to reconstruct habitat distribution through space. We downloaded a comprehensive database (>4100) of latest Cretaceous dinosaur occurrences from the Paleobiology Database and combined this with a high-resolution atlas of palaeogeography. A time series analysis of species distribution models was developed from the early Campanian to the late Maastrichtian of North America. The ecological niches modelled on available outcrop area through time show a decline for herbivorous taxa from the Campanian to the Maastrichtian, with an initial increase followed by a slight decline for tyrannosaurids, mirroring trends based on previous diversity analyses. However, when continental projections are considered, taking into account the poorly sampled eastern half of North America, these patterns shift dramatically, with an overall increase in habitat suitability between the Campanian and Maastrichtian for all three clades. This novel approach suggests that dinosaur diversity was not in decline in the lead-up to the K-Pg boundary, and highlights the impact of spatial bias in interpreting macroevolutionary dynamics.

NEW LATE DEVONIAN LUNGFISHES FROM GREENLAND MORPHOLOGICALLY AND PHYLOGENETICALLY BLUR THE D-C BOUNDARY

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Three small lungfish specimens were collected in 1987 from the late Famennian of Greenland by the Copenhagen-Cambridge expedition that also found the iconic specimens of *Acanthostega*. Study of these lungfish specimens including by microCT scanning shows that they probably all belong to the same species. They show a number of derived characters uncommon in Devonian taxa, but which are more typical of Carboniferous examples. The most conspicuous of these is a long-stalked parasphenoid with a diamond-shaped anterior plate. In the new specimens, the stalk is about twice the length of the plate, as in many Carboniferous genera. This feature is also shown in an isolated parasphenoid figured by Lehman in 1959 and attributed to the early Famennian *Oervigia*. Future studies of his material are planned to determine whether our new material is also a species of *Oervigia*. Bayesian and parsimony-with-implied-weighting phylogenetic analyses place the new material among Carboniferous forms, notably with *Ctenodus*. Devonian taxa normally range through the base of the tree, with Carboniferous forms clustering together towards the top. In our analyses, only the Devonian *Nielsenia*, also from Greenland, falls within the Carboniferous cluster. Our new material thus demonstrates that more derived forms prefiguring those of the Carboniferous did exist in the Devonian, and help to fill the morphological and phylogenetic gaps and blur the stratigraphical boundary implied by the end-Devonian mass extinction. Some lungfish lineages, as with some tetrapods, appear not to have been as seriously affected by that extinction event as others.

COMPARATIVE SKULL BIOMECHANICS IN *VARANUS* AND *SALVATOR* '*TUPINAMBIS*'

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The lizard species *Salvator* '*Tupinambis*' *merianae* and *Varanus ornatus* evolved independently in South America and Africa but share similar ecology and feeding behaviour, despite having notable differences in their skull structure. *Tupinambis* has a compact, relatively short and wide snout, whereas that of *Varanus* is more slender and narrow. In addition, a postorbital bar (POB) is present in *Tupinambis* but absent in *Varanus*, and the former lacks the mid-frontal suture that is present in the latter. Here, we explore the biomechanical significance of these differences using 3D computer-based mechanical simulations based on micro-computed tomography, detailed muscle dissections, and in vivo data. First, we simulated muscle activity and joint-reaction forces

during biting using Multibody Dynamics Analysis. Then, the forces calculated from these models were used as an input for Finite Element Analysis, to investigate and compare the strains of the skull in these two species. The effects of the presence/absence of structures, such as the POB, were investigated by constructing artificial models which geometry was altered. Our results indicate that strains in the skull bones are lower in *Tupinambis* than in *Varanus*, in particular at the back of the skull. The presence of a POB clearly reduces the strains in the bones during posterior biting in *Tupinambis*, but not in *Varanus*. Our results hence highlight how the morphological differences between these two taxa affect the mechanical behaviour of their respective skulls during feeding.

ECOMORPHOLOGICAL DISPARITY AND EVOLUTION OF MARINE REPTILES OF THE SUB-BOREAL JURASSIC SEAWAY

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The dominant consumers in Jurassic ocean ecosystems were distantly related clades of reptiles secondarily adapted to an aquatic lifestyle. Stratigraphic and fossil evidence suggests that, like their modern counterparts, different lineages such as plesiosaurs, ichthyosaurs, and thalattosuchian crocodylomorphs were able to coexist in the same environment. As diet and trophic specialisation are the main drivers for convergent evolution in modern aquatic environments, it is possible that marine reptiles occupied analogous ecological roles now held by cetaceans, sirenians, and large fishes such as sharks. However, these comparisons, supported by qualitative observations, have rarely been tested in a quantitative way. In this study, we aim to rectify this using the rich fossil assemblage from the Middle-Late Jurassic Sub-Boreal Seaway (Callovian–Tithonian, 164–145 Mya). Using multivariate analyses, we analysed a novel dataset of continuous and discrete functionally relevant characters from the dentition and lower jaws of 62 specimens. Our results show that the transition from the Middle to the Late Jurassic involved a significant decrease in functional disparity for pliosaurids and teleosaurids, and an increase for ichthyosaurs and metriorhynchids. Late Jurassic metriorhynchids and ichthyosaurs shifted towards regions of ecomorphological space vacated by groups that had declined from the Middle Jurassic. Combined with novel fossil evidence from the so called ‘Corallian Gap’ (a poorly investigated interval of the Oxfordian deposited in between the fossil-rich Callovian and Kimmeridgian formations), our results indicate that a significant marine faunal turnover – maybe linked to environmental perturbations – affected the marine ecosystems through the early Late Jurassic.

A RE-EXAMINATION OF *OROVENATOR MAYORUM* USING µCT DATA, AND ITS CONSEQUENCES FOR EARLY AMNIOTE PHYLOGENY

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Orovenator mayorum, from the early Permian (Sakmarian) of Oklahoma, has been described as the earliest representative of Neodiapsida, a clade that includes dinosaurs and birds, snakes, lizards, crocodiles and turtles. High-resolution CT scans of the two

known specimens of this taxon reveal novel anatomical data. These include the arterial pathways in the basicranium and palate, the osseous canal enclosing the nasolacrimal duct, and well preserved septomaxillae. Exceptional detail of the cranial sutural anatomy is evident, including unusual medial buttressing on the lacrimal and maxilla which indicate a high structural integrity of the anteorbital region. By combining the elements of both specimens we have been able to reconstruct most of the skull in virtual 3-D, including a complete palate and basicranium.

Several features of *Orovenator* are shared with Varanopidae, a generally accepted stem-ward clade of pelycosaur-grade synapsids. Substantial similarity between early diapsids and varanopid synapsids has previously been noted: four taxa currently assigned to the Varanopidae were originally described as diapsids (*Archaeovenator*, *Heleosaurus*, *Apsisaurus*) or archosauromorphs (*Mesenosaurus*). However, our study suggests that these similarities are greater than previously appreciated, raising questions about deep phylogenetic divergences within amniotes. Application of the new data on *Orovenator* into an existing phylogenetic matrix intended to discriminate between varanopids and diapsids resulted in an unresolved consensus. This has prompted work on a novel phylogeny, with greater taxonomic scope, to provide a working hypothesis for the interrelationships of Permo-Carboniferous amniotes.

EVOLUTION OF BODY SIZE IN CROCODYLOMORPHA IN A MULTI-REGIME EVOLUTIONARY LANDSCAPE

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Body size is strongly related to physiology and ecology, and its evolution has been studied intensely for many animal groups. Crocodylomorphs occupy the intermediate–large range of body sizes among extant tetrapods, and have a rich and diverse fossil record, ranging in size from less than 30 centimetres to over 10 metres in length. To investigate crocodylomorph body size evolution, we used maximum-likelihood to fit macroevolutionary models to body length data within a phylogenetic context. We focused on non-uniform Ornstein-Uhlenbeck (OU) models ("SURFACE" model). Under an OU process, lineages are attracted towards an adaptive trait optimum (theta, θ) through time. SURFACE allows multiple adaptive regimes (i.e. shifts in trait optima). We also fitted other models, and conducted analyses using alternate body length proxies, tree topologies and time-calibration methods, to assess the influence of analytical choices on results. The SURFACE model fit best to our data, suggesting convergent evolution of body size among macroevolutionary adaptive zones. Although different trees identify regime shifts in phylogenetically distinct positions, we recognized some shared patterns. For instance, non-Mesoeucrocodylia crocodylomorphs maintained relatively small sizes (θ = 0.646 m), and experienced no or few shifts, thriving until the Late Cretaceous. During the Late Jurassic and Cretaceous, crocodylomorph body size disparity increased, with a high number of regime shifts, particularly within Notosuchia and Thalattosuchia. Another important regime shift, towards larger body sizes (θ = 5.561 m), occurred in the lineage

leading to extant crocodylians (Eusuchia), potentially related to an adaptive radiation of the group after the Cretaceous-Paleogene extinction.

USING COMPUTATIONAL FLUID DYNAMICS TO ANALYSE THE HYDRODYNAMIC PROPERTIES OF FOSSIL MARINE REPTILES

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Various groups of reptiles recolonised aquatic environments and became apex predators of the Mesozoic seas; among them were the iconic ichthyosaurs, plesiosaurs and mosasaurs. During their evolution, their anatomies were subject to strong selective pressures imposed by the physical constraints of water, resulting in adaptations to locomotion such as the streamlining of body shapes, and the transformation of cursorial limbs into paddles or hydrofoils. Until recently, the functional impact of these morphological changes has been difficult to study due to the lack of an objective, physics-based quantitative method.

Computational fluid dynamics (CFD) is a state-of-the-art engineering tool used to simulate fluid flows and to calculate the forces resulting from fluid-solid interactions. Here, I will present a case study in which the effect of body plan evolution on the hydrodynamic properties of ichthyosaurs is analysed by means of CFD. Full-body reconstructions of various specimens were created using 3D modelling software, and the total drag and lift as well as the contribution of the limbs to these forces were evaluated. The results demonstrate that changes in the body plan of ichthyosaurs – from the narrow and elongated basal forms to the deep-bodied and highly streamlined parvipelvians – did not contribute to drag reduction, contrary to what has classically been suggested. The ecological relevance of these results will be discussed.

Building upon this experimental strategy, we aim to evaluate the degree of functional convergence in hydrodynamic performance in the most derived species of Mesozoic marine reptiles, and also between these and aquatic mammals.

THE FIRST VIRTUAL CRANIAL ENDOCAST OF A POROLEPIFORM FISH AND THE EVOLUTION OF THE DIPNOMORPHA

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The Dipnomorpha include the extinct Porolepiformes, in addition to *Powichthys* and *Youngolepis* and the extant Dipnoi (lungfish). As sister group to the Tetrapodomorpha, the Dipnomorpha hold a valuable place in our understanding of early sarcopterygian evolution. With complete cranial endocasts now known from most other stem sarcopterygian groups including actinistians and tetrapodomorphs (which bracket the Dipnomorpha), a thorough

understanding of the porolepiform endocranium remains one of the last pieces in the puzzle towards understanding evolution of the neurocranium in stem sarcopterygians.

We present the first virtual cranial endocast of a porolepiform fish (*Glyptolepis paucidens*) demonstrating that it displays predominantly primitive sarcopterygian endocast characters including: lack of a bifurcation of the olfactory nerves, separate pineal and parapineal recesses, circumvention of the nasal capsule by the profundus nerve, and sessile olfactory bulbs. The union of the orbitonasal canal and the nasal capsule is consistent with that seen in *Powichthys*, *Youngolepis* and other porolepiforms*,* however circumvention of the nasal capsule by the profundus resembles the dipnoan *Dipterus*, contrasting with the state observed in other porolepiforms and *Powichthys.*

Inconsistent with the general primitive nature of the endocast seen in *Glyptolepis* is the large, curved hypophyseal recess, a feature shared with *Powicthys* but unlike *Youngolepis*. Furthermore, *Glyptolepis* displays ventral expansion of the telencephalon - a character thought to be derived within the Dipnoi.

This new data enhances our understanding of brain and sensory evolution in sarcopterygians. In particular, it shows conservatism in stem Porolepiformes contrary to the disparate morphology of their sister-group the Dipnoi.

THE FORT MCMURRAY NODOSAUR – A THREE-DIMENSIONAL DINOSAUR FOSSIL WITH PRESERVED SCALES, PIGMENTS, AND STOMACH CONTENTS

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In the spring of 2011 a surprising discovery was made – a three-dimensional dinosaur fossil in the marine sediments of the Aptian–Albian age Clearwater Formation in northeastern Alberta, Canada. During the previous 20 years, two ichthyosaurs and nine plesiosaurs had been recovered from the tar sand mines in the area north of the town of Fort McMurray. Soon after the carcass arrived at the seabed, a very dense, well-cemented concretion grew around the carcass, and protected the specimen from subsequent crushing from overburden pressure over the next 112 million years. The only damage to the specimen occurred at the instant of discovery by heavy equipment, resulting in the loss of the tail and parts of the limbs. The concretion had the unfortunate side-effect of preventing permineralization of the armour and skeleton, leaving the fossil extremely soft. The unscavenged, uncrushed specimen shows all the dermal armour in place and in association with the underlying skeleton. Patterns of inter-locking, large polygonal scales, preserved as carbon films, demonstrate the relationships between osteoderms and squamation. Fossil pigment allows for the interpretation of a counter-shading on the body. The specimen arrived at the seabed on its back, and the rotting viscera collapsed downwards to rest on the spine. A collapsed, football-sized volume of densely packed, pea- to grape-sized concretions are interpreted to be animal's last meal. The preserved armour and skin are so extensive that skeletal details are largely hidden from view.

FUSION IN THE VERTEBRAL COLUMN OF THE PACHYOSTEOMORPH ARTHRODIRE *DUNKLEOSTEUS TERRELLI* ('PLACODERMI')

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Fusion in the vertebral column occurs normally in jawed vertebrates, with structures like the sacrum and pygostyle providing rigidity, support and increased area for muscle attachment. The synarcual represents the fusion of the anterior part of the vertebral column and occurs in a number of jawed vertebrates, including a variety of placoderms and chondrichthyans. Placoderms are an entirely fossil group of armoured fishes (Silurian–Devonian), resolved to the base of the jawed vertebrate clade, with vertebrae comprising neural and haemal arches composed of perichondral bone. The placoderm synarcual preserves substantial developmental information from anterior (oldest) to posterior, where new vertebrae are incorporated.

A subadult specimen of the pachyosteomorph arthrodire *Dunkleosteus terrellli* preserves vertebral elements showing varying degrees of anteroposterior fusion along the vertebral column. Synarcuals are rarely preserved in this group, and micro-CT scanning of this synarcual provides details of a transitional zone of vertebral fusion, providing unprecedented information on how each vertebra is modified and incorporated into the synarcual. All elements in the synarcual retain vertebral identity, showing less fusion overall, more comparable to other arthrodires such as *Compagopiscis*. By comparison, synarcuals of other taxa such as ptyctodont placoderms, batoids, holocephalans (Chondrichthyes) and mammals (syncervical) show more complete fusion of vertebral elements.

EARLY CAMBRIAN OSTRACODERMS AND THE TRIALS AND TRIBULATIONS OF TOTAL EVIDENCE DATING

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The origin of jawed vertebrates is a formative episode in evolutionary history. Key to understanding this important interval are the armoured jawless 'ostracoderms', the relationships among which have previously been considered either in terms of clade intrarelations, or interrelations among clade exemplars. Thus, the monophyly of the putative ostracoderm plesions have yet to be adequately tested, principally because of computational limitations surmounted in the last decade. We constructed a supermatrix of 560 characters and 240 taxa, which we analysed using the MK likelihood model. The ensuing trees were compared using Bayes factors. Our results support the majority of ostracoderm clades, but resolve galeaspids and heterostracans as paraphyletic grades of

stem-gnathostomes, and stem-vertebrates, respectively. Finally, we considered the role of time in topology estimation, using the fossilized birth-death model (FBD). This approach resolved heterostracans, thelodonts and anaspids as a single clade, while suggesting that ostracoderms evolved in the earliest Cambrian. This result conflicts strongly with the fossil record, suggesting that the FBD method may incorrectly estimate divergences of extinct taxa. Taken together, these results suggest that the consensus of early vertebrate relations, underpinned by the last 40 years of cladistics, does not stand up to deeper scrutiny afforded by likelihood-based phylogenetics.

THE RECENT NOW: POST-MEDIEVAL WOOD MICE

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During the post-medieval era in Western Europe, arable land expanded and agricultural practices homogenised ecological and landscape diversity. There were also highly increased rates of vertebrate disappearance and extinction. Anthropogenic species such as wood mice (*Apodemus* spp.) have persisted, despite the increased intensity in human impacts. An analysis of *Apodemus* mandible shape variation in France does however show a dramatic shift in mandible shape between the end of the 16th century and the present day. This change is more distinctive than all the mandible shape variability present in the preceding 12,000 years. A biomechanical model suggests that present-day wood mice are less capable of producing a higher bite force. Implications for function probably include a reduced dietary range, for example due to restricted access to diverse natural resources or the increasing availability of homogenous anthropogenic resources. The changes in landscape structure therefore appear to have imposed new functional requirements on native species. These results indicate that there are pervasive changes in ecosystem function in response to human impacts from the post-medieval era. Comprehensive datasets of archaeological small mammal material therefore provide crucial insight into organism function as well as the dramatic impact of ecological and landscape changes during this transformative episode of the European Holocene.

OPPORTUNITIES IN DISASTERS: MOLECULAR EVIDENCE FOR THE RAPID RADIATION OF SNAKES FOLLOWING THE CRETACEOUS-PALEOGENE MASS EXTINCTION

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Mass extinction events have shaped global biodiversity throughout Earth's history. The most recent major mass extinction, at the Cretaceous-Paleogene (K-Pg) boundary, took place 66 Mya and has been particularly well studied. This event witnessed the demise of non-avian dinosaurs, pterosaurs, and mosasaurs, amongst numerous other major groups. However, it also provided an opportunity for significant ecosystem restructuring, and has been suggested to have stimulated the rapid diversification of mammals, teleosts, frogs, and birds in its aftermath. The influence of the K-Pg mass extinction on the evolutionary history of snakes is less well understood, however. To address this understudied topic, we used a molecular clock approach to show that Alethinophidia, the clade comprising the majority of modern snake diversity and disparity, also underwent a rapid diversification in the aftermath of the K-Pg mass extinction event. We used a novel supermatrix representing 169 species coded for up to 52 loci, and a new set of 42 phylogenetically and stratigraphically constrained fossil calibration points. Divergence time analyses were performed under a variety of parameterisations in PhyloBayes and PAML, and numerous outgroup taxa were included to control for rate heterogeneity within the ingroup. Our inferred association between the K-Pg event and the rapid diversification of Alethinophidia provides further evidence of the importance of this mass extinction in shaping Earth's modern vertebrate faunas. Our analyses also imply that crown snakes only explored arboreality after the K-Pg, suggesting some degree of ecological filtering induced by the mass extinction event.

THE ROLE OF MINIATURISATION FOR CRANIAL FUNCTION ACROSS THE CYNODONT-MAMMALIAFORM TRANSITION

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The evolution of mammals from cynodonts is a key event in vertebrate history and is characterized by a number of modifications to the cranial skeleton. This is most prominently expressed in the emergence of a novel jaw joint and the reduction of the mandible to a single tooth-bearing bone in crown mammals. These skeletal changes are generally thought to be allied with increasing cranial strength in response to a more powerful and complex jaw musculature, and the evolution of a more 'efficient' feeding system.

Using an integrated suite of digital reconstruction, visualization and biomechanical

modelling techniques (FEA, MDA), we studied six key taxa (including *Thrinxaodon*, *Probainognathus*, *Morganucodon*, and *Hadrocodium*) across the cynodont-mammaliaform transition. This allowed testing the hypothesis that during feeding the cranial skeleton of cynodonts and mammaliaforms experienced progressively lower magnitudes of stress and strain and increased bite forces.

Results show a slight decrease in average stress and strain across taxa, but do not support a large-scale trend for the increase of cranial strength towards crown mammals. However, we find that a reduction in size of the cranial system, as observed across the cynodont-mammaliaform transition, results in opposing trends of reducing bite forces, but also a substantial reduction of compressive and tensile stresses in the jaw joint. This suggests that presumed changes in the loading regime and/or the cranial morphology did not act as the main trigger for the emergence of a novel jaw joint. Rather, miniaturisation provided an evolutionary environment, in which substantial morphological modifications were possible.

HIPS, TIPS AND SWEET SWEPTBACK RAYS: LOOKING BEYOND TRADITIONAL CRANIAL CHARACTERS IN PACHYCORMIFORMES

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A focus on cranial characters for determining relatedness is a predominant trait in many datasets, however this overemphasis can lead to distortion from sampler bias. We report on revised analyses of pachycormids - a key group within Actinopterygii, as part of the Holostei-Teleostei transition, which display a phyletic trend towards reduced skeletal ossification with the increased adult size of a pachycormid taxon. This reduced preservation potential for the axial skeleton makes it difficult not to base phylogenetic assumptions primarily on the limited skull material present. However, pachycormids show a remarkable conservatism in their dermatocranial anatomy, the few differences being useful for showing the separation of genera, but of little utility in working out broader intrafamilial relationships. The combination of a paucity of postcranial characters in the Late Cretaceous pursuit predator *Protosphyraena* with a poor knowledge about the skulls of suspension-feeding pachycormids (SFPs) had led to the absence of Early Cretaceous predatory pachycormids being interpreted as indicating a ghost lineage between *Protosphyraena* and the European Upper Jurassic taxa *Orthocormus* and *Hypsocormus* over an almost 50-million-year gap. However, the inclusion of several features from the pectoral and pelvic fins, supplemented by splanchnocranial characters, produces a much clearer picture that questions the traditional perception of a single carnivore lineage: *Protosphyraena* emerges as secondarily carnivorous from the SFPs' tribe, mirroring 130 years of misidentification of North American *Bonnerichthys* specimens as *Protosphyraena*. Confirmation of this will rely on the further recovery of data concerning the skull morphology of SFPs.

HIGH DIVERSITY OF SMALL DINOSAURS PRECEDING THE CRETACEOUS-PALEOGENE (K-PG) MASS EXTINCTION

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Dinosaurs dominated terrestrial ecosystems for over 100 million years, before disappearing at the end of the Cretaceous. Based on the fauna of the Western Interior of North America, it has been assumed that latest Cretaceous faunas were low in diversity and dominated by large species, consistent with the hypothesis that there was a decline in dinosaur diversity preceding the K-Pg boundary that left dinosaurs vulnerable to extinction. However, small dinosaurs are rare and tend to be understudied, raising the possibility their apparent low diversity is an artefact of sampling and study biases. Here, it is shown that alongside the giant *T. rex* and *Triceratops*, a diverse fauna of small dinosaurs thrived in the late Maastrichtian, including previously unrecognized taxa of Dromaeosauridae, Troodontidae, Caenagnathidae, Alvarezsauridae, Thescelosauridae and Leptoceratopsidae. Total dinosaur diversity includes at least 29 species ranging from 2 kg to 50,000 kg, occupying carnivorous, herbivorous, insectivorous, and piscivorous niches. An analysis of functional diversity, using a combination of behavioural characters, morphological characters chosen for functional significance, and body size shows that ecological niche occupation increased rather than decreased from the Late Campanian to the Late Maastrichtian in the Western Interior, driven by the immigration of new taxa such as alvarezsaurids and titanosaurians. These patterns reject the hypothesis of a dinosaur decline, and suggest that the dinosaur fauna remained ecologically diverse until the end of the Cretaceous. These findings are consistent with a catastrophic extinction at the end of the Maastrichtian coinciding with, and driven by, the Chicxulub asteroid impact. The extinction of small dinosaurs also suggests that while size was a major contributing factor, size selectivity alone cannot explain dinosaur extinction.

SPATIOTEMPORAL PATTERNS IN FOSSIL SAMPLING BIAS AND THEIR IMPACT ON UNDERSTANDING THE EVOLUTIONARY HISTORY OF TERRESTRIAL CROCODYLOMORPHS

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The 24 species of living crocodylians are the remnants of a once much more diverse and widespread clade. Crocodylomorpha has an ~230 myr evolutionary history that was punctuated by a series of radiations and extinctions. Whereas previous studies have reconstructed sampling-standardised crocodylomorph diversity, the completeness of the fossil specimens themselves provides additional information that is not captured in those approaches. We compiled a dataset of all taxonomically diagnosable, non-marine species (393) of Crocodylomorpha, including fossil occurrences of extant taxa. Based on the number of phylogenetic characters (484) that can be scored for all known fossils of each species, we calculated a completeness value for each taxon. Average species completeness is 55%, and this value is largely consistent within subgroups (e.g. Crocodylia, Notosuchia, non-neosuchians) and for different body size classes, suggesting

no significant biases across the crocodylomorph tree. In general, average completeness values are higher in the Mesozoic (60%) than the Cenozoic (50%). Completeness decreases across the Cretaceous/Paleogene boundary, which might explain why an uncorrected census of taxonomic diversity shows a crash at this mass extinction, whereas a sampling standardisation approach reveals little change in overall standing diversity. There is no evidence for a Pull of the Recent effect, with lower average completeness during the last ~10 myr, although many extant taxa are identified based on very incomplete fossil remains. Spatiotemporal sampling bias impedes our understanding of some Mesozoic radiations, including Neosuchia and Notosuchia, whereas divergences within Crocodylia based on molecular data are generally in close agreement with the fossil record.

GRABBING EVOLUTION BY THE THROAT: FUNCTIONAL REGIONALISATION OF THE AVIAN CERVICAL COLUMN

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Birds have evolved powerful forelimbs that are used primarily in flapping flight. This has rendered these appendages less useful for environmental manipulation than in many of their dinosaurian antecedents. Reliance on the head and neck for feeding and environmental interaction places high selective pressure on cervical form-function, potentially explaining the diversity in neck morphology seen in birds. However, to-date there has been no systematic study of morphological diversity in the avian neck and its correlation with feeding habits. This study uses a combination of three-dimensional geometric morphometrics (GMM) and qualitative character coding to assess regionalisation within the cervical column of a wide variety of extant birds. These species represent a large diversity of feeding (carnivores, seed eaters) and functional (swimmers, flyers and terrestrial) ecology, cervical count (12–17) and body size. Results provide strong support for 5 cervical subregions (axis, anterior, middle, midposterior, posterior) in all species. The atlas subregion appears to show the strongest signal, with the axis (cervical 2) being clearly separate in all studied birds, possibly owing to its function into head stabilisation. Other subregions with a reasonably stable cervical count (anterior and posterior) also display a clear functional role. The remaining 2 regions (middle, midposterior) show much variability in cervical count between species (middle 2–6 cervicals, midposterior 1–4 cervicals). These results suggest that whilst the underlying *Hox* genetics may restrict avians to 5 cervical subregions, expansive variability in the middle and midposterior regions allow the cervical columns of birds to adapt to many different functional ecologies, and may be responsible for the large variety of neck morphologies observed in extant Aves.

PTEROSAUR WING BONE GEOMETRY AND ITS RELATIONSHIP TO PNEUMATICITY AND PALAEOECOLOGY

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Pterosaurs are typically portrayed as having extremely thin-walled wing bones, much thinner than birds, which is assumed to lower mass, assisting large bodied forms in take-off and flight. However, there is a trade-off as thinner-walls are more likely to buckle or bend. Smaller, basal taxa are called 'thick'-walled, while more derived pterodactyloids are described as thinner-walled, suggesting a size constraint. Here I present the first phylogenetically-grounded cross-clade study of pterosaur wing bone geometry. I test the phylogenetic affinity of pterosaur bone thickness, and its relationship to both pneumaticity and palaeoecology, using 120 wing bones. Cortical thickness (t) and diaphyseal radius (R) of wing bones was measured in order to characterize variation using R/t and K-values (inner to outer bone radius), and bending stiffness was estimated using second moment of area (I). Contrary to previous studies, wing bone thickness does not carry a phylogenetic sign al, nor vary consistently between or within groups. R/t values similar to those seen in modern birds are common, with relatively few large-bodied pterodactyloids reaching extreme values upwards of 15. Incorporating size reveals a phylogenetic signal in K and R/t values. Bending stiffness varies from 30 to over 1 000 000 m4, increasing with bone size. These data show that smaller-bodied forms, were resistant to impact, compression and buckling, typical of animals frequently taking-off and landing. Conversely, larger pterosaurs were optimized for mass reduction and bending resistance, essential for wings under high loads. R/t values may indicate if a bone was pneumatic, but more data is needed.

NEW ONYCHODONTID (OSTEICHTHYES; SARCOPTERYGII) REMAINS FROM THE MIDDLE DEVONIAN OF MOROCCO

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Onychodontids are a specialized and phylogenetically important group of marine sarcopterygians (lobe-finned fishes), probably closely related to coelacanths. However, they are among the least well-understood groups of early osteichthyans (bony fishes). The principal reason for this is their partly cartilaginous and therefore perishable endoskeleton, which causes the bones of the head to disarticulate and scatter after death.

A new onychodontid species from the Eifelian (Middle Devonian) of Morocco was found 40 years ago but it was only preliminarily described. These fossil remains can be attributed to a single individual and new preparation of the specimen has revealed new features and bones that were not previously known. Dermal skull bones are well preserved and allow a partially complete reconstruction of the snout, cheek and skull roof. Moreover, endoskeletal branchial and fin bones are exceptionally preserved, adding to our knowledge of early osteichthyan endoskeleton.

Preliminary phylogenetic placement supports its basal position among onychodontids,

enabling to test evolutionary scenarios among the clade. This new species, along with well-preserved onychodontid fossils from Euramerica (*Strunius* from Germany) and Gondwana (*Qingmenodus* from China and specially *Onychodus* from Australia) adds to our knowledge of these elusive fishes. The Moroccan specimen, representing the first occurrence of onychodontids from Africa, constitute important material from a new Gondwanan locality that would furnish key information not only on onychodontid morphology and interrelationships, but also on their paleobiogeographical distribution and Devonian faunal affinities between Euramerica and Gondwana.

THE BIOMECHANICAL SIGNIFICANCE OF THE RODENT MANDIBULAR INCISOR "ROOT" – A FINITE ELEMENT ANALYSIS STUDY

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Rodents are an order of mammals characterised by a distinctive masticatory apparatus which includes a pair of enlarged and continually growing incisors, a feature termed diprotodonty. Diprotodonty is present in all living and extinct rodents and has independently evolved in a phylogenetically diverse range of non-rodent mammals; including the aye-aye, a primate which we have previously shown to be highly convergent in skull morphology to rodents.

This study examined the functional significance of the incredibly long rodent-like incisor. A sample of four rodents, and the non-rodent diprotodont aye-aye, were segmented to exhibit incrementally shorter internal incisor lengths, with variant models containing a solid crypt and a hollow crypt, and examined using finite element analysis to examine the resultant differences in principal strains. The primary aim of this study was to elucidate whether the internal length of the incisor is functionally significant to the resistance of mechanical forces encountered during incision.

The findings of this research indicate that strain increases substantially as a consequence of shortening the internal length of the incisor, with strain increasing by up to 35%. This study thus finds that the long internal incisor plays a substantial role in the resistance of bending forces, both by itself, and in tandem with an arch-like mandibular shape - itself a result of a long and curved internal incisor. Consequently, this study proposes that the evolution of these features together aid in strengthening the rodent-like mandible against the repetitive loadings and high forces encountered during the iconic rodent behaviour – gnawing.

A VIRTUAL RECONSTRUCTION AND VOLUMETRIC MASS ESTIMATE OF AL288-1, *AUSTRALOPITHECUS AFARENSIS*

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Fossil body mass estimation is a well-established practice within the field of physical anthropology. Previous studies have relied upon traditional allometric approaches, where the relationship between skeletal dimensions and body mass in a range of modern taxa is used predictively. The lack of relatively complete skeletons has limited the potential application of alternative mass estimation techniques, such as volumetric reconstruction, to fossil hominins. Yet across vertebrate palaeontology, volumetric approaches are increasingly predicting values for fossil body mass very different to those estimated by traditional allometry. Here we present the results of a virtual reconstruction exercise for the iconic hominin AL288-1 and the calculation of its body mass, created using a combination of differing morphometric techniques. These reconstructions represent working hypotheses of the morphology of AL288-1, based upon what is currently known about *Australopithecus* anatomy.

The convex hull technique relies upon identifying a predictable relationship between the 'shrinkwrapped' volume of the skeleton and known body mass in a range of modern taxa, and subsequent application to an articulated model of the fossil taxa of interest. Here, our calibration dataset comprises whole body CT scans of 15 species of modern primate. Application of the convex hull technique to *A. afarensis* results in a relatively low body mass estimate of 20.1kg (95% prediction interval 13.3–30.6kg). A sensitivity analysis on the thorax, performed by 10 and 20% expansion of this area, suggests that the heaviest of previous body mass estimates would require the thorax to be expanded to an unlikely extent.

THE DENTARY OF *WAREOLESTES REX* AND NEW FOSSIL MAMMAL MATERIAL FROM THE MIDDLE JURASSIC OF SKYE, SCOTLAND

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The Middle Jurassic was a pivotal time for many vertebrate groups: recent research suggests mammals experienced a surge in ecological diversity at this time. However, vertebrate fossils from the Middle Jurassic are rare. Until now, Middle Jurassic mammals in the UK came almost exclusively from Bathonian deposits in England, while globally the most complete specimens are mainly found in China. Ongoing fieldwork on the Isle of Skye suggests this locality is of international significance for microvertebrate skeletal remains. So far, Skye has yielded skeletal associations and fragmentary material including early mammals, tritylodontids, salamanders and basal squamates.

We report the most complete specimen of the Middle Jurassic morganucodontan *Wareolestes rex*, from the Bathonian Kilmaluag Formation of Skye, Scotland. The

specimen was digitally reconstructed using microCT scan data. It comprises a partial left dentary with two erupted molars, one unerupted molar, and three unerupted premolars. Empty alveoli for a canine, p1 and p3 are also present.

Wareolestes was previously known from four isolated molars from Kirtlington, England, and there was debate over the position of the holotype tooth as an upper or lower molar. Comparing our new material with the holotype, we support the original diagnosis of the holotype as a lower molar, most likely m1. In the Scottish specimen, unerupted and erupted premolars, and presence of permanent molars, supports diphyodonty in *Wareolestes*. This has previously been suggested for other morganucodontans. Damage to the dentary of *Wareolestes* means questions remain regarding the sequence of replacement along the tooth row in this genus.

A NOVEL PHYLOGENY FOR THE HETEROSTRACI: EVOLUTIONARY RELATIONSHIPS OF EXTINCT JAWLESS VERTEBRATES ON THE GNATHOSTOME STEM

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Heterostracans - the largest clade of extinct bony jawless vertebrates (ostracoderms) - are a key member of the jawed vertebrate (gnathostome) stem, and are thus fundamental to our understanding of early vertebrate evolutionary patterns. There are many different and disparate clades within the Heterostraci, but all are united in having a single pair of external branchial openings. Phylogenetic relationships of the Heterostraci are poorly understood, meaning the plesiomorphic state for heterostracans and most likely vertebrates as a whole is unknown. Here, we propose a new phylogeny including all described heterostracan genera (137 taxa), including taxa from Pteraspidiformes, Cyathaspididae, Psammosteidae, Amphiaspididae, Traquariaspididae and the problematica. Our results indicate the Cyathaspididae are paraphyletic and the Psammosteidae fall within the Pteraspidiformes. Inclusion of quantitative characters improves the resolution of phylogenetic trees for this morphologically homogenous group. This novel phylogeny provides a framework to investigate major evolutionary transitions such as dispersal histories. Using the stratigraphical occurrence of taxa, we also investigate the stratigraphical congruence of phylogenies and find that heterostracans originate in Laurentia and disperse into other palaeocontinents from this provenance.

MORPHOLOGICAL DATA PARTITIONING AND PHYLOGENETIC SIGNAL IN RODENTS

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Different morphological character partitions (e.g., teeth vs. postcrania) sometimes vary in the extent to which they reflect phylogenetic history. They may also vary in terms of their impact on deep vs. superficial nodes. For example, in at least some clades, dental data might reflect accurate, historical signal among recently diverged species and genera, but become noisier with deeper nodes and older divergences. Here, we measure how signal

provided by different partitions in Glires (Rodentia + Lagomorpha) varies with node depth across a tree, from superficial clades at the tips to basal clades near the root. Glires comprises over 40% of mammalian species and has an excellent fossil record and our understanding of their phylogenetic history has greatly improved in recent years. This makes it a good sample with which to examine hard-tissue partitions. By measuring median distances between unambiguous character changes and the root of a tree across several morphological partitions, we found no significant differences between the depths of clades supported by the different data partitions in Glires. Finer detail suggests a slight bias in axial skeleton characters to support more basal clades and for braincase and basicranium characters to optimize as synapomorphies for clades near the tips of the tree. Overall, our study suggests that commonly used, hard-tissue morphological characters in Glires contain at least some signal to support clades throughout the tree, both deep and superficial.

HOW DO MECHANICAL LOADS INFLUENCE CRANIAL SHAPE AND FUNCTION DURING DEVELOPMENT?

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The shape of the vertebrate skeleton is dictated by a mixture of genetic patterning and environmental influences. Mechanical loading via muscle activity is required for normal skeletal development, including in the skull. Despite this, we have little idea of the extent to which mechanical loads control embryonic and adult morphology and how this subsequently influences skull function. To address this question we used zebrafish, a model vertebrate system, to investigate how disrupted mechanical loading modifies craniofacial form and function. We compared control fish developing normally to fish anaesthetized for varying time periods between 3-5 days postfertilization and mutant fish that lack adductor musculature. Control fish began to voluntarily open and close their mouths at days 4 to 5. Removal of muscle loads at days 4 to 5 resulted in abnormal Meckel's cartilage and jaw joint shapes. Removal of loads earlier during development had little effect on element shape and joint formation. After recording muscle fibres, fibre area and estimated muscle force, we used finite element modelling to reconstruct strains within the developing cartilages. Mutant and anesthetized jaws functioned differently to control jaws, and when muscle-induced strain is absent, cells on the medial side of the joint changed orientation. Our results suggest that muscle-induced strain regulates cell orientation at the developing joint and that biomechanical loading via adductor muscle contraction plays a key role in normal zebrafish jaw formation. Modification of the developmental loading environment leads to cranial shape changes and offers a mechanism by which evolutionary shape change can occur.

DIFFERENCES BETWEEN HARD AND SOFT DATA IN PHYLOGENETIC ANALYSES

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Heterogeneity of phylogenetic signal is often tested for and accounted for when analysing molecular data, but not when analysing morphological data. Differences between types of morphological data will prove problematic, especially if those differences align with the missing data biases intrinsic to the fossil record. Here we demonstrate through meta-analysis of 59 empirical morphological datasets that significant differences exist between the phylogenetic signal conveyed by 'hard' biomineralized characters and 'soft' characters (i.e. bones, teeth and shells versus myology, integument, neurology etc.). Those differences are demonstrated through application of partition heterogeneity tests (incongruence length difference test and incongruence relationship distance test). Furthermore, hard and soft morphological partitions are found to differ in their consistency relative to independent molecular trees. Differences between readily fossilizable and less fossilizable characters could prove problematic for drawing evolutionary inferences from fossil data, especially in those clades in which the hard character partitions have been demonstrated to be less consistent with molecular trees than the soft character partitions (mammals, bivalves). Other clades are found to exhibit fewer differences (non-acanthopterygian fishes, gastropods) or demonstrate elevated consistency of the hard character partitions on molecular trees relative to soft character partitions (birds, potentially including dinosaurs, and acanthopterygian fishes). In which case, the later clades maybe a more appropriate focus for macroevolutionary studies that utilize fossil data. In all cases it will be necessary to consider the role that missing data plays in shaping empirical data, and consider the differences that exist between morphological modules.

TESTING ADAPTIVE RADIATION SCENARIOS IN MARINE FISHES BY COMBINING PHYLOGENOMIC AND PALAEOBIOLOGICAL DATA

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Adaptive radiation scenarios have been invoked to explain the diversity of some of the best studied groups of organisms (e.g., Rift lake cichlids, Hawaiian Silversword Alliance, passerine birds). Under the most traditional adaptive radiation model numerous lineages start diverging within a brief period of time from an ancestral adaptive type, with each new lineage filling an available ecological niche; subsequently this rapid initial morphological evolution is replaced by relative stasis due to most available niches having already been filled. A number of recent studies, based on molecular phylogenies, questioned the generality of this model and found little evidence of an early burst of morphological diversification in most studies. For most of these clades, however, it is not known if inclusion of the palaeodiversity would have modified the results. I will compare the results of our study of several major groups of marine teleosts, such as tetraodontiforms (puffers, triggerfishes and allies), carangoids (jacks, remoras), acanthuroids (surgeonfishes, luvar) and sparoids (seabreams, emperors and allies). All of these groups possess a rich fossil record - mostly known from European sites - which to date has rarely been used in evolutionary studies. I will show how the results based on extant taxa and those based on

extant plus extinct species differ, and how inclusion of fossil data can alter the conclusion of studies based on molecular phylogenies.

IMPROVING MORPHOLOGICAL CHARACTER CHOICE IN PHYLOGENETIC INFERENCE - DATA FROM MODERN CROCODILIANS

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Molecular phylogenies are increasingly reliable, with larger datasets and improved analytical techniques. Morphological phylogenies often continue to conflict with them, due to convergent morphological evolution masking phylogenetic signal and the difficulties of character delineation. While molecular analyses can be increasingly relied upon for modern taxa, phylogenetic placement of fossil taxa must continue to rely on morphology, and this raises the concern that phylogenetic placement of fossils will remain less accurate. In order to assess how better to avoid these problems, homoplasy of characters from a recent morphological phylogenetic analysis including modern crocodilians was assessed against a tree based on recent molecular phylogenies. The relative homoplasy of different character groups was assessed using the consistency index, retention index and rescaled consistency index. Cranial characters were significantly less homoplastic than postcranial characters ($p < 0.05$), as were multistate characters compared to binary characters. Differences between braincase characters and the rest of the skull, and between “naturally” delineated characters and other characters were nonsignificant. Morphological characters in the matrix were reassessed first hand. Those characters in which homology across taxa within a state was less doubtful tended to be consistent with the molecular tree. This was confounded by less robust characters possibly having been created/scored with a pre-existing grouping in mind; these characters were nonhomoplastic but could not be reliably observed. This work may begin to assist in improving fossil archosaur, and potentially vertebrate, phylogenetics; further work with a wider taxonomic scope is required.

RANGE OF MOTION AND HYDRODYNAMIC IMPLICATIONS OF THE LONG-NECK IN PLESIOSAURS

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Plesiosaurs are iconic extinct marine reptiles, and they possessed some of the longest necks among all vertebrates. The biomechanical implications of such a long neck on fundamental functions such as forward swimming remain relatively understudied. This study explored range of motion between cervical vertebrae from two plesiosaur species (*Mureanosaurus* sp. and *Cryptoclidus eurymerus*) using 3D digitization and modelling. The 3D models were manually aligned and then rotated until contact with the posterior vertebrae in order to measure maximal lateral, dorsal and ventral bending limits. Both species showed greatest bending dorsally (10.7° and 10.2° mean intervertebral rotations for *Muraenosaurus* and *C. eurymerus*). Mean ventral rotations were 5.3° and 7.5°, and lateral rotations 7.9° and 7.5° for *Muraenosaurus* and *C. eurymerus*. Summed for all vertebrae in the neck, this implies total dorsal/ventral/lateral flexion of 428°/212°/316° for

Muraenosaurus and 326°/240°/240° for *C. eurymerus*. While soft tissue would reduce these ranges considerable, this provides an osteological maximum. Additionally, computational fluid dynamics (CFD) was used to simulate hydrodynamic effects of the long neck during forward locomotion. The CFD analyses included simulations of an idealised 3D plesiosaur model with the neck bent at different degrees (0-90) and locations (head, middle, and evenly). Intuitively, the CFD results showed higher drag as degree of bending was increased (0°; Cd = 0.041 vs. at 90°; Cd = 0.204). Combining digitization of real fossil specimens with idealized simulation can help shed light on the biomechanical implications of the long neck in plesiosaurs.

THE COMPLICATED AND SURPRISINGLY EARLY ORIGIN OF THE PTERODACTYLOID BAUPLAN

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The origin of the pterodactyloid bauplan from that of non-monofenestratan ('rhamphorhynchoid') pterosaurs involved extensive anatomical changes and had profound consequences for the evolutionary history of Pterodactyloidea, a clade that dominated the aerial realm throughout the Cretaceous. This important evolutionary transformation, about which almost nothing was known for almost two centuries, is now rapidly coming into focus thanks to a plethora of new pterosaur fossils from the Middle and Upper Jurassic of South America, Europe and China. So far, however, these finds have largely been considered in isolation from each other and few have been thoroughly evaluated. Phylogenetic analysis, combined with improved stratigraphic data for all potentially relevant taxa including putative non-pterodactyloid monofenstratans (NPMs) and the oldest known pterodactyloids (e.g. *Liaodactylus*) was used to generate a new map of the anatomical transformations and temporal history of the non-monofenestratan–pterodactyloid transition. Evolution of the pterodactyloid skull construction predates the Middle Jurassic, but remains almost completely undocumented by fossils. *Liaodactylus* reveals that innovation in pterodactyloid skull anatomy and the appearance of derived features was well underway prior to the Upper Jurassic. *Douzhanopterus*, a derived NPM, demonstrates that elongation of the metacarpus and reduction of the tail and fifth toe (classic pterodactyloid synapomorphies) also predates the Upper Jurassic, but disjunction in the degree of their development across taxa is not consistent with simple explanations such as 'adaptation for flight'. Overall, late Early to early Late Jurassic pterosaurs were much more diverse and had a far more complex evolutionary history than heretofore recognised.

GLIDE ANALYSIS AND BONE STRENGTH TESTS INDICATE POWERED FLIGHT CAPABILITIES IN HATCHLING PTEROSAURS

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Pterosaur embryos and 'hatchling' specimens show a surprising level of skeletal development including well-ossified skeletons and large wings. This has prompted

interpretations of pterosaurs as being flight-capable from the earliest ontogenetic stages, contrasting them against the majority of other flying animals, living or extinct. Though popular, this hypothesis is not universally accepted. Some authors propose that pterosaurs only became flight capable once they reached 50% of maximum size, explaining a slowing of growth rate in later ontogeny as metabolic resources were diverted into an energy-demanding form of locomotion. We investigated these hypotheses through glide performance and wing bone strength analysis on hatchling-grade specimens of two pterosaurs, *Pterodaustro guinazui* and *Sinopterus dongi*. We found that hatchling pterosaurs were excellent gliders, but with a wing ecomorphology more comparable to powered fliers than obligate gliders. Bone strength analysis shows that hatchling pterosaur wing bones are structurally identical to those of larger pterosaurs and – because of their very low body masses – their bending strength relative to body weight is very high, comparable to or exceeding the greatest values estimated for larger, more mature pterosaurs. Hatchling pterosaurs are thus as mechanically adapted to powered flight stresses as other pterosaurs, if not moreso. Together with our glide tests, this result supports interpretations of hatchling pterosaurs as flight-capable. Size differences between pterosaur hatchlings and larger members of their species dictate differences in wing ecomorphology and flight capabilities at different life stages, which might have bearing on pterosaur ontogenetic niching.

SVPCA POSTER ABSTRACTS

A REVISION OF THE MORPHOLOGY AND SYSTEMATICS OF GEOEMYDIDS (TESTUDINES: CRYPTODIRA) FROM THE MESSEL PIT QUARRY

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We present preliminary results of our revision of European Eocene geoemydids, concentrating on two putative species from the Konservat-Lagerstätte of the Messel Pit quarry, in the state of Hesse, Germany. The two species, herein referred to as *Palaeoemys kehreri* and *Palaeoemys messeliana*, are the dominant components of the abundant and well-preserved testudinoid material from Messel, being represented by nearly 100 specimens, often complete shells with associated skeletal material. Despite this, there are not clear diagnoses for these species or a firm knowledge of their relationships within geoemydids, in large part because of the extensive morphological variation within the populations, and the difficulty of finding phylogenetically informative characters for geoemydids in general. We aim to remedy that situation with new descriptions based on observations of multiple specimens from the two largest collections for these species, which we integrate in the context of more general geoemydid relationships thanks to a larger body of data that we have collected from the extant species of the group.

QUANTIFYING THE QUALITY OF THE MESOZOIC MARINE TETRAPOD FOSSIL RECORD

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Studying the completeness of the fossil record is important for understanding how various biotic, taphonomic and human sampling biases affect our knowledge of macroevolutionary process and our ability to reconstruct past biodiversity patterns. The marine fossil record has traditionally been considered more complete than the terrestrial due to the increased likelihood of fossil preservation. Previous work has shown that the skeletons of some marine reptiles, such as ichthyosaurs and plesiosaurs, are typically more completely preserved than groups of contemporary terrestrial fossil reptiles such as sauropodomorphs. A surprising negative correlation between skeletal completeness and sea level has also been recovered. The study of other groups of marine reptiles is needed to test reveal how universally applicable these results are. Here, we study skeletal completeness of three groups of Triassic marine reptiles: placodonts, nothosaurs and pachypleurosaurs. These groups typically have smaller body sizes than ichthyosaurs and plesiosaurs and have distinct ecological preferences, offering a contrast to these previously studied groups. We calculated the skeletal completeness metric (SCM), which scores the proportion of a complete skeleton a single specimen preserves, for all valid species of these groups. Provisional results show higher completeness values than for terrestrial reptiles, similar to the patterns documented for ichthyosaurs and plesiosaurs. Ongoing work will examine the correlations between SCM values in these groups and taxic

diversity, sea level, and specific preservational environments. The future inclusion of more fossil groups, such as pistosaurs and thalattosaurs, will offer a complete view of marine reptile fossil completeness.

QUANTIFYING THE COMPLETENESS OF THE BAT FOSSIL RECORD

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Assessing temporal changes in fossil record completeness is important for identifying taphonomic and sampling biases that make inferring biological signals directly from the fossil record problematic. Chiropterans (bats) evolved soon after the Cretaceous-Palaeogene mass extinction, but are not found in the fossil record until c. 14 Myr later, and are generally thought to have a poor fossil record. Here we quantify the completeness of the bat fossil record by calculating the previously defined skeletal completeness metric (SCM) and character completeness metric (CCM) for >400 valid species.

Skeletal proportions used to calculate SCM were determined from (1) the surface areas of bones from 2D scientifically-informed skeletal reconstructions and (2) from bone volumes of a CT-scanned 3D bat skeleton. Completeness scores were compared to each other and to species richness through geological time, between different depositional environments, and to scores from other tetrapod groups.

Significant differences occur between SCM scores based on 2D and 3D methods of determining body proportions. Isolated teeth are the predominant elements occurring in the bat fossil record, resulting in consistently low SCM scores, but are diagnostic enough for taxonomists to identify significant diversity even at times of low completeness. This is supported by CCM scores being significantly higher than SCM. Temporal peaks in completeness generally result from the presence of Könservat Lagerstätten. An exception is the Pleistocene, which shows high species richness and completeness scores despite lacking Lagerstätten. This is likely due to the preservation of cave deposits, which are rare or absent in older time intervals.

EVALUATING THE PERFORMANCE OF MORPHOLOGICAL PARTITIONS IN RECOVERING AVIAN EVOLUTIONARY HISTORY

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Despite increased use of genomic data in phylogenetics, morphological information remains important in resolving evolutionary relationships, particularly for rare and fossil species where molecular data is unavailable. Accordingly, methods of phylogenetic reconstruction using morphological data have been widely discussed in recent literature, including whether the use of sophisticated model-based methods is better than traditional parsimony. Another important issue with molecular data, however, is the nature of the morphological characters themselves. Selection and evolutionary lability can make some sets of characters more prone to homoplasy than others. Moreover, when these characters evolve in semi-autonomous modules, they have the potential to overwhelm

genuine phylogenetic signal contained within the data. The present study uses a meta-analysis approach to compare osteological and soft-character partitions in birds to determine whether these partitions contain different levels of homoplasy when compared to a molecular phylogeny. We find that soft-tissue characters are less consistent with molecular data in general, but that they are more consistent with this phylogeny for a single, large morphological dataset. This may partly reflect different evolutionary rates at different taxonomic levels, but generally osteological data appear to track evolutionary history better than soft characters in birds.

THE ANATOMY AND RELATIONSHIPS OF *EUCAMEROTUS FOXI* (DINOSAURIA, SAUROPODA) FROM THE EARLY CRETACEOUS OF ENGLAND

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Eucamerotus foxi is a macronarian sauropod from the Wessex Formation (Early Cretaceous, Barremian) of the Isle of Wight. It is represented by NHMUK R2522, a partial dorsal neural arch, and differs from other known sauropods by the presence of a stout robust prezygaparapophyseal lamina (PRPL) which bifurcates distally. NHMUK R90 are a pair of dorsal vertebrae also from the Wessex Formation which have been designated as paratypes of *E. foxi*. Both NHMUK R2522 and NHMUK R90 have traditionally been regarded as either basal titanosauriformes or of brachiosaurid affinities. Here, phylogenetic analysis using the LSDM recovered NHMUK R90 as a non-titanosaurian somphospondylan nested in a clade made up of ((*Tastavinsaurus* (*Chubutisaurus*, *Angolatitan*, NHMUK R90)) though Bremer support for this group was low. Analyses recovered *E. foxi* as a neosauropod of uncertain affinities with little resolution throughout the tree. NHMUK R90 is recognised as being distinct from *E. foxi* based on the lack of a robust distally bifurcated PRPL and is likely representative of a new sauropod taxon. *Eucamerotus foxi* is here retained as a valid species of basal macronarian.

CHARACTER COMPLETENESS OF TEMNOSPONDYL AMPHIBIANS: A NEW METHOD TO ASSESS OUR KNOWLEDGE OF CHARACTER CHANGES THROUGH TIME

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Changes in the completeness of fossil specimens can alter the amount of observable character states per species, and therefore affect our macroevolutionary interpretations. The quality of the tetrapod fossil record has previously been quantified as the proportion of phylogenetic characters that can be scored for an individual species. This character completeness metric (CCM) scores how much information is available for each species but not how well we understand each specific character and how knowledge of these characters changes along lineages. Here, we present an alternate implementation of the CCM which focuses instead on examining how completely known individual characters are through time. By time binning character scores of cladistic matrices, a proportional completeness of each individual character per time bin can be calculated. This can be

used to determine mean overall CCM through time for each matrix, but can also be used to examine variation in completeness across different partitions of cladistic characters, such as between different skeletal regions.

We apply this method to the fossil record of temnospondyl amphibians using all previously published phylogenetic matrices focused solely on the group. We examine whether varying levels of character-specific completeness through time may offer a potential explanation for poorly constrained areas of temnospondyl interrelationships. Preliminary results show that mean temnospondyl character completeness is consistently very high for most time bins (~60–100%), with little relative fluctuation through time. However, the most character-rich matrix illustrates there are significant differences in completeness through time between different portions of the temnospondyl skeleton.

PATTERNS OF ALPHA DIVERSITY FOR PHANEROZOIC TERRESTRIAL VERTEBRATES

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The fossil record of local-scale taxonomic richness offers the strongest test of whether ecological limits regulate long-term patterns of diversification. Terrestrial diversity equilibria are particularly controversial, yet long-term patterns of local richness on land are remarkably poorly constrained. We show that Phanerozoic non-flying tetrapod diversification is largely characterized by asymptotic patterns of local richness. Richness increases occur primarily in the Carboniferous, when terrestrial ecosystems were being assembled, and around the Cretaceous-Paleogene boundary. Major clades (dinosaurs, squamates, mammals) exhibit early rises in local richness followed by protracted periods of stability. Observed patterns of stasis in local richness over long timescales cannot result from key fossil record biases. They strongly contradict models of unbounded terrestrial diversification, but are consistent with ecological limits to diversity.

TOOTH DAMAGE, LOSS AND REPLACEMENT IN PYCNODONT FISHES

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Pycnodonts are an extinct group of neopterygian fishes that lived from the late Triassic (Norian) to Eocene (Lutetian–Ypresian). They were primarily marine and often reef dwelling, with heterodont dentitions, including crushing teeth on the vomer and prearticular bones. Two species, *Pycnodus maliensis* and *Pycnodus zeaformis* from the Late Palaeocene/Early Eocene of Mali have highly unusual dentitions, which appear to show tooth replacement where damage or loss of teeth has occurred. Micro-CT scans of the fossils show that small, round teeth, very different to the molariform teeth they have replaced, appear to have developed at an abrasion or wound surface; possibly constituting wound-healing tooth addition. We are comparing tooth replacement mechanisms in a

range of modern fish, to infer those present in these species. The vomer of the common sea-bream (*Pagrus pagrus*) is morphologically very similar, but we found the replacement mechanism to be different, with replacement teeth located beneath and associated with the functional tooth, as normal for actinopterygians. Our micro-CT scans of the Atlantic salmon (*Salmo salar*) show seemingly irregular positioning of new teeth in spawning males, the replacement mechanism possibly relating to that of the pycnodonts. Cichlids also present an unusual replacement pattern, in that tooth type (crushing or not) can be epigenetically induced in an individual's lifetime,depending on the availability of hard and soft food. Next steps are therefore to search for genetic control mechanisms in these and other vertebrates that could produce the unusual morphology seen in the pycnodont fossils.

NEW DATA ON THE OPHTHALMOSAURID BASICRANIUM

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Ophthalmosaurids were the stratigraphically youngest ichthyosaur group and the morphology of the basicranium is important for phylogeny, especially the amount of basioccipital extracondylar area. However, this character has some challenges for phylogenetics, because its presence is inconsistent at the family and subfamily level. Although articulating to the basioccipital, the basisphenoid is rarely found, as few specimens preserve both elements. Material from the Slottsmøya Member Lagerstätte (SML), Spitsbergen, can contribute to an evaluation of basicranium characters. Excavations (2004–2012) in the SML (Tithonian–Berriasian) have yielded 29 ichthyosaur specimens. Seven are previously described with a new specimen presented here, as well as *Cryopterygius kristiansenae* basicranial material. The size relationship between the basioccipital and basisphenoid for SML material and 16 specimens from other localities was calculated in order to establish whether there is any systematic variation useful for phylogenetic relationships or functional morphology.

The new specimen preserves basicranium, jaw remains, an articulated dorsal vertebral column and pectoral girdle. It shows similarities to SML genera *Janusaurus* and *Palvennia*, but also to the widespread *Arthropterygius*, with possible biogeographical implications. Material from the *Cryopterygius kristiansenae* holotype includes basioccipital, basisphenoid and stapes. The subfamily Ophthalmosaurinae is characterized by a large extracondylar area, but the supposedly ophthalmosaurine SML assemblage includes specimens with zero and another with a very extensive extracondylar area. The basisphenoid morphology also varies, most importantly in size and shape of the pterygoid processes. The results from the calculation of basioccipital-basisphenoid pairs indicate that the size relationship is stable within Ophthalmosauridae and considerably less variable than the morphology.

DELTAPODUS FOOTPRINTS PROVIDE EVIDENCE OF STEGOSAURS ON ISLE OF SKYE (SCOTLAND, UK) IN THE MIDDLE JURASSIC

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Although the Middle Jurassic (ca. 174–164 Ma) marks a pivotal time of diversification within dinosaur lineages, the global dinosaur body fossil record during this time is sparse. Dinosaur footprints supplement this scrappy body fossil record. Two new in-situ dinosaur track sites from the Lealt Shale Formation of the Great Estuarine Group (Bathonian) on the Isle of Skye present a diverse ichnoassemblage that includes footprints associated with ornithopod, theropod, and thyreophoran track makers. The tracks are predominantly impressions in a dark gray, thinly laminated shale with abundant desiccation cracks that were later infilled with casts of a tan bioclastic limestone. While the theropod and ornithopod tracks are consistent with previous footprint discoveries on Skye, a short quadrupedal trackway consisting of five prints of *Deltapodus* morphology is of particular interest as the first thyreophoran trackway from this area. Although the overall morphology is consistent with the type *Deltapodus* tracks from Yorkshire, the Skye *Deltapodus* tracks are significantly smaller (with an average length 16 cm). The tracks extend the known range of *Deltapodus*, which is primarily known from Western Europe, the western United States, and China and are the most northerly occurrence of this ichnogenus. These tracks provide evidence that stegosaurs were present on Skye during the Middle Jurassic and underscore the Isle of Skye's potential as location for better understanding this period of geologic history.

TERRESTRIAL TETRAPOD DIVERSITY & BIOGEOGRAPHY ACROSS THE CARBONIFEROUS/PERMIAN BOUNDARY

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Major patterns of Palaeozoic tetrapod diversity continue to be surrounded by widespread disagreement, stemming from the ongoing debate on how spatial and temporal sampling biases affect our ability to decipher genuine estimates of palaeodiversity. Previous studies suggested that the late Carboniferous Rainforest Collapse (CRC) significantly impacted tetrapod diversity and drove the development of endemism. However, these studies failed to account for variations in sampling. To facilitate more robust investigations of Carboniferous–early Permian tetrapod diversity and biogeography, we developed a new global species-level dataset (>400 species from 520 unique localities) within the Paleobiology Database. Our analyses of species richness and alpha diversity reveal a fluctuating pattern distinct from previous estimates showing a continuous rise in taxonomic diversity across this interval. Subsequent analyses that attempt to correct for sampling indicate that sampling biases strongly affect interpretations of diversity change, particularly in the Carboniferous. To examine the effect of the CRC on tetrapod communities we used a newly-devised biogeographical network method which uses phylogenetic data to quantify

biogeographic connectivity between distinct geographic regions. Contrary to the existing hypothesis that habitat fragmentation resulting from the CRC drove endemism, our analysis suggests that cosmopolitanism increased markedly following the CRC. Our study compels a revision of the current view of early tetrapod diversity and the response of tetrapod communities to the end Carboniferous Rainforest Collapse. Additionally, we highlight the caveats associated with estimating Paleozoic terrestrial diversity and the impact of sampling biases on estimates of diversity.

CORRELATES OF MAMMALIAN TOOTH ERUPTION PATTERNS

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Variation of tooth eruption and replacement patterns among mammalian species have been hypothesised to be related to various factors, including phylogenetic relatedness, diet, crown height, brain size, and pace of growth. For example, Schultz's rule predicts that replacement teeth (second generation teeth) tend to erupt earlier in respect to the molar teeth in relatively slow growing mammals. Here, we present a study which compares tooth eruption patterns across the whole breadth of Mammalia and relates potential changes of these patterns to a range of variables that have previously been hypothesised to influence tooth eruption. Our dataset comprises more than 1000 specimens, representing ontogenetic series of 40 mammalian species, including marsupials, xenarthrans, afrotheres, euarchontoglires, and laurasiatherians. These data show that the variability of tooth eruption patterns is influenced by phylogenetic relatedness, i.e., certain patterns are only found in certain clades. This includes a correlation between at least some life history patterns and "slow" development (i.e., Schultz's rule) in primates. Further, variation of body mass appears to affect variation of tooth eruption patterns across all species. Our study will help to elucidate the evolution of tooth eruption patterns on a broad taxonomic scale, not only within certain clades, and will therefore likely also inform inferences about extinct taxa.

AN ICHNOLOGICAL STUDY OF THE SALOP FORMATION (UPPER CARBONIFEROUS) OF SHROPSHIRE

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The terrestrial red beds of the Alveley Member of the Salop Formation in Shropshire preserve the most important collection of Upper Carboniferous vertebrate trace fossils in the UK. The tetrapod footprints from the Alveley Member have received recent study, but the ichnoassemblage also includes tetrapod body impressions (cubichnia) and arthropod trackways (repichnia) that have received little examination. Here, we conduct the first comprehensive examination of these neglected elements. Analysis of the material was undertaken through comprehensive cataloguing; measurement and qualitative examination of the fossil morphology; creating 3D computer models using photogrammetry; and comparison to stratigraphically equivalent ichnoassemblages. The vertebrate body and resting impressions were identified as having been produced by a

diplocaulid nectridean amphibian, based on an impression interpreted as having been formed by the distinctive boomerang-shaped head. This is the second known body impression of the group, in addition to a specimen described previously from Germany under the name *Hermundurichnus* Walter and Werneburg, 1988. Preservation of this material was polyphase, with cubichnia and repichnia elements, providing potential insights into previously hypothesised life habits for longhorned diplocaulids. A diverse assemblage of arthropod trackways was also identified, including six ichnospecies. The occurrence of these ichnofossils together with previously studied elements of the Alveley Member increase understanding of terrestrial environments and vertebrate evolution during the Late Carboniferous.

PALAEOPATHOLOGICAL TRENDS IN JURASSIC MARINE REPTILES

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Palaeopathology, the study of disease and injury in ancient animals, has contributed significantly to our current understanding of population dynamics and disease in extinct taxa. The principal aim of this study is to investigate whether there are significant differences in pathologies between Jurassic crocodilians, plesiosaurs and ichthyosaurs. This study also aims to describe pathological specimens of particular interest in order to develop our knowledge of bone healing in these animals. Observations showed a large assortment of bite marks in Kimmeridge Clay Formation (Upper Jurassic) and Oxford Clay Formation (Middle to Upper Jurassic) material, particularly on the appendicular region of plesiosaurs. Key findings also included well-healed fractures, predominantly in ichthyosaur and plesiosaur ribs, which indicated that Jurassic marine reptiles were resilient against trauma. However, complications arising from a non-fatal bite on a plesiosaur humerus also showed a susceptibility towards infection after injury. A defect of vertebral formation and segmentation, causing congenital scoliosis of the spine, was described for the first time in a marine reptile specimen. This may have had severe implications for the animal's swimming capabilities. Though there is some evidence to suggest differences in pathology type and location in Jurassic marine reptile groups, a strong emphasis can also be placed on the extraordinary ability of these animals to heal bones subsequent to trauma. This may reflect the high growth rates suggested for some of these clades, as well as the many ecological pressures faced from predation and competition in their respective habitats

IDENTIFICATION OF SMALL CARNIVORE FOSSILS USING BRAIN ENDOCASTS

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One classification trait that distinguishes species is the shape of the brain; more specifically, shapes of the sulci differ in many types of carnivore. Because of these differences, this brain-form classification method may be used to identify fossil species. In this study, brain form was studied using the cranial fossils of small carnivores (unidentified specimens) and extant species from the Mustelidae (*Mustela itatsi*, *Martes melampus*, *Meles meles*) and Mephitidae (*Spilogale putorius*, *Mephitis mephitis*) families. Using these

materials, the study considered whether the analysis of brain form is an effective method of fossil identification. The materials used herein included silicone brain endocasts. Identification focused on the sulci in the cerebrum's surface and involved a comparison of the materials. Differences among species were identified in three sulci: the lateral sulcus (la), located in the upper temporal lobe of the cerebral hemisphere; the suprasylvian sulcus (ss), located in the middle temporal lobe of the cerebral hemisphere; and the sylvian sulcus (sy), located in the lower temporal lobe of the cerebral hemisphere. As a result of comparison, the small carnivore fossil morphotypes were more similar to the sulci of the Mephitidae rather than those of the Mustelidae. Based on the identification of molars, the small carnivore fossils may be those of a spotted skunk (*S. putorius*). Therefore, the target fossils had the same result as the identification by the molars.

RESOLVING PHYTOSAURIA: A TRIFOLD CLADISTIC APPROACH

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Historically the in-group phylogeny of Phytosauria has proven problematic, due to multiple 'wastebasket taxa', a limited set of characters, and poor transatlantic sampling. Recently, advances in parsimony analysis have permitted incorporation of alternative data types with the potential to help elucidate phytosaur phylogeny. Here we investigate the in-group relationships of Phytosauria and the impacts of discrete, continuous and geometric morphometric (GM) character coding methods on tree topology. Extensive first-hand study of European and American specimens, intensive investigations to identify novel characters, and uniting characters from previous analyses has generated the most taxonomically comprehensive cladistic dataset of phytosaurs to date, with an almost two-fold increase in phylogenetic information scored for each taxon. Alongside traditional phylogenetic methods, data are coded and analysed as non-discretised continuous ranges and landmark-based representations of shape using the software TNT, tackling issues of arbitrary or subjective character scoring. Continuous and GM character variants were systemically incorporated into a base discrete character matrix, resulting in four well resolved tree topologies showing the effect of data type on phylogeny. Nodes were collapsed using an arbitrary Bremer support score to prevent artificial over-resolution due to implied weights. The combination of all three coding techniques did not generate best tree resolution, this was instead achieved by their discrete counterparts alone. This raises questions of whether standard support tests are appropriate for these data types. Continuous and GM coding is limited due to higher dependence on complete morphology, and GM especially as it is cumbersome to implement and greatly increases analysis time.

RECORDING THE UNCOLLECTABLE WITH LOW COST LOW TECH: SUCCESSFUL PHOTOGRAMMETRY IN THE FIELD USING A MOBILE PHONE TO CREATE DIGITAL 3D MODELS

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There are many different ways to record the three-dimensional morphology of a specimen in detail. Most techniques rely on expensive, cumbersome and delicate equipment requiring a power supply. However, if a very large and heavy fossil or geological feature in the field cannot easily be removed to a museum or is in danger of imminent loss it would be very useful to be able record the three-dimensional morphology of the find accurately and in detail there and then with readily available low-cost equipment and with simple techniques.

Fortunately, experimentation has shown that photogrammetry using a standard 5-megapixel mobile phone digital camera can produce very good quality digital 3D models of specimens in the field (such as short dinosaur trackways) that are useful for research. Unlike some scanning methods this also provides a photographic overlay to the morphological model creating, effectively, a 3D photographic record of the specimen and surrounding context.

Even specimens larger than 1 m^2 can be recorded to a level of sub-millimetre resolution with such a device in reasonable lighting conditions and if the relevant photographic techniques and image processing techniques are well understood. The software required to convert the photographs into 3D models is readily available and low cost. Current mobile phone cameras can even produce results that are better than digital SLR cameras in some low light conditions and they are improving every year. As most people have a mobile phone with them on fieldwork, with a little training anyone can undertake scientifically useful 3D scans.

A QUANTITATIVE EVALUATION OF PHYSICAL AND DIGITAL APPROACHES TO CENTRE OF MASS ESTIMATION

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Centre of mass is a fundamental anatomical and biomechanical parameter. Knowledge of centre of mass is essential to inform studies investigating locomotion and other behaviours, through its implications for segment movements, and on whole body factors such as posture. Previous studies have estimated centre of mass position for a range of organisms, using various methodologies. However, few studies assess the accuracy of the methods that they employ, and often provide only brief details on their methodologies. As such, no rigorous, detailed comparisons of accuracy and repeatability within and between methods currently exist. This project therefore applied three methods common in the

literature (suspension, scales and digital modelling) to three 'calibration objects' in the form of bricks, and to three birds to determine centre of mass position. Application to bricks enabled conclusions to be drawn on the absolute accuracy of each method, in addition to their relative values. Application to birds provided insights into the logistical challenges of applying these methods to more complex, biological specimens. For bricks, we found that, provided appropriate repeats were conducted, the scales methods yielded the most accurate predictions of centre of mass (within 1.49 mm), closely followed by digital modelling (within 2.39 mm), with results from suspension being the most distant (within 38.5 mm). Scales and digital methods both also displayed low variability between estimates, suggesting they can accurately and consistently predict centre of mass position. Our suspension method resulted not only in high margins of error, but also substantial variability, highlighting problems with this method.

NEW SPINOSAURID DINOSAUR FINDS FROM THE WESSEX FORMATION (WEALDEN GROUP, EARLY CRETACEOUS) OF THE ISLE OF WIGHT

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The discovery in Surrey of *Baryonyx walkeri* in 1983 was a highly significant event which reinvigorated the study of British dinosaurs, at a time when theropod material from the Wealden was usually assigned to the genus *Megalosaurus*. In the 1990's the Museum of Isle of Wight Geology (subsequently Dinosaur Isle Museum) acquired many new specimens, including material from the theropod dinosaurs *Neovenator salerii* and *Eotyrannus lengi*; however, vertebrae, a phalanx and denticle counts of isolated teeth, confirmed the presence of a *Baryonyx*-like spinosaurid on the Island.

The Wessex Formation exposed on the Isle of Wight is the richest dinosaur assemblage in Europe, with a diverse flora and fauna dominated by dinosaurs. Systematic sieving of the plant debris beds has yielded many baryonichid teeth. However, recently a number of collectors have made significant finds including a substantial proportion of the crania of at least two individuals on the Island's south-west coast. The area is heavily collected and unfortunately some material has not come into the collection; however, many significant finds are now in the care of Dinosaur Isle Museum.

Besides the palaeoenvironment and cranial osteology, future research will include a comprehensive study of the dental morphology, including tooth counts, replacement and variation; CT scanning to establish the endocranial anatomy and examination of the relationship of the trigeminal nerve to the numerous pits on the premaxillae, maxillae and dentaries. Our studies will test the hypothesis that the new material can be assigned to *Baryonyx walkeri*.

REVIEWING THE VERTEBRATE FOSSIL RECORD

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The vastness of the vertebrate fossil record and its literature makes any effort to review it in entirety a difficult task; 'a review' is understood to be a work that discusses the evolution and diversity of a group, drawing in knowledge on taxonomy, morphology, ecology and distribution, with representative illustrations. Existing reviews of the entire vertebrate record have mostly been designed with teaching in mind and have focused on groups, trends and processes deemed of interest to students. As goes more specific reviews, some groups (Mesozoic dinosaurs in particular) are frequently reviewed; others are afflicted by their association with idiosyncratic authors, others have only been given partial treatment, and others are woefully under-represented. Biographical information on vertebrate palaeontologists themselves is scattered. An additional issue is that several excellent volumes (notably the Handbook volumes) are prohibitively expensive, rare or otherwise hard to obtain. Cenozoic fishes – in particular actinopterygians, the largest and richest vertebrate radiation – remain essentially untouched and it might not be obvious to non-specialists just how rich the fish record is. Indeed, an enormous number of lineages scarcely known to experts on modern fishes are present in the fossil record.

The result of this skewed coverage is that both popular and technical perception of the vertebrate fossil record is biased. Not only are there a huge number of groups that fail to attract students, a large number of research questions relevant to these groups remain un- or under-investigated because so few researchers are aware of their existence.

SYSTEMATICS OF LATE CRETACEOUS EUROPEAN ANKYLOSAURS: THE IMPORTANCE OF THE DERMAL ARMOUR

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Dermal armour composition and/or the morphology of a specific osteoderm can be diagnostic at generic or even species level in many lineages of armoured tetrapods. In ankylosaurs, besides cranial ornamentation, the cervical and pelvic armour elements are the most complex, diagnostic and easily recognizable parts. Whereas cervical elements are usually fused in half-rings bearing plates and/or spikes, pelvic armour shows a diverse composite of oval, polygonal or rounded osteoderms being completely or partially fused or unfused.

The ankylosaur record from the Upper Cretaceous of Europe is relatively poor, and is known only by a few occurrences from Cenomanian and Santonian to Maastrichtian deposits, but osteoderms are present in most assemblages. Two different morphotypes of cervical half-rings, representing *Hungarosaurus tormai* and *Struthiosaurus* sp., are present in the Santonian of Hungary. The half-ring of the early Campanian *S. austriacus* differs from the Hungarian remains. From the Upper Cretaceous of the Ibero-Armorican landmass cervical half-rings are known from Cruzy (southern France), Laño and Chera (Spain). Though they are generally similar to each other and to those of the Central European

elements, the shape of the dorsally projected plates and the number and morphology of the ossified elements between the plates are different. In addition, the recognition of massive conical spikes both in *Hungarosaurus* and in the Austrian ankylosaur material suggests that the latter is also represented by two different taxa. This suggests that ankylosaur diversity during the last 20 myr of the Late Cretaceous European archipelago was greater than previously thought.

ELEPHANT DUNG, CHEWED ANTLERS, WEATHERED BONES: DOCUMENTING A UNIQUE TAPHONOMIC COLLECTION

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The Antony John Sutcliffe Collection is a unique taphonomic reference collection held within the Department of Earth Sciences at the Natural History Museum (NHM). Sutcliffe was the Curator of Fossil Mammals at the NHM from 1957 to 1987, during which time he collected a large assemblage of modern comparative vertebrate material, including complete skulls, bones, teeth and soft tissues (skin and faeces) of numerous species from across the world including sites in East Africa, Canada, Alaska, Siberia and northwest Europe. Sutcliffe studied Pleistocene mammals and was particularly interested in the alterations to their remains after death and how they come to be fossilised, i.e., their taphonomy.

The specimens were either collected during Sutcliffe's own fieldwork or gifted to him by international colleagues, and are often accompanied by detailed notes on their provenance and original letters of donation.

After a preliminary study in 2013, and given the value of the collection for future taphonomic studies, a curatorial project ran from 2015 to 2017 aiming to document the entire collection on EMu (the museum's collection management system), recording the anatomy, taxonomy, previous and new locations within the museum, and any associated documentation of over 1500 specimens. Photographs of each object were included and all specimens have been registered, safely repacked and rehoused at Wandsworth museum store, where they are now accessible to researchers. The specimens have the potential to form curated taphonomic reference standards for use by researchers around the world.

THE MOST COMPLETE ANKYLOSAUR SKULL EVER FOUND IN THE WESSEX SUB-BASIN (LOWER CRETACEOUS) OF THE ISLE OF WIGHT

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Ankylosaur remains are frequently recovered from the Lower Cretaceous Wealden deposits of the Isle of Wight, although the vast majority of these fossils represent post-cranial elements and osteoderms. The rarity of ankylosaur cranial material means any new specimens are important for understanding the morphology, palaeoecology and evolution of these taxa. Here we describe a well-preserved partial ankylosaur cranium recovered with associated ankylosaur remains from the Wessex Formation at Compton Bay. This is the most complete ankylosaur skull ever recovered from the Wessex Sub-basin and is now held at Dinosaur Isle Museum (DI), Sandown, IOW. A highly water worn specimen held at the Sedgwick Museum of Earth Sciences was found at Chilton Chine in the early 1990s and assigned to cf. *Polacanthus*, and the two crania are compared here.

The specimen consists of the posterior part of the basicranium and skull roof including the proximal paraoccipital processes, occipital condyle and basal tuberosity. Both skulls share characters including the position of some of the foramina exiting the endocranium and lateral curvature of the skull roof. The DI skull differs from the Sedgwick specimen by the presence of a well-defined, notched border of the supraoccipital, flat rostal-caudal dorsal cranial surface, the occipital condyle being more bulbous and angled more ventrally, a well-defined nuchal shelf and being smaller and less robust. Differences between the specimens may be due to sexual dimorphism, ontogeny or they may represent different taxa.

APPLYING THE FOSSIL RECORD OF CROCODYLIA TO ASSESS EXTINCTION RISK TODAY

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The 24 living species of crocodylians (crocodiles, alligators, caimans and gharials) are the sole remnants of a once much more diverse group that evolved 250 million years ago (Ma), with crocodylians first appearing in the fossil record 80 Ma. Approximately 50% of living crocodylians are vulnerable to extinction or critically endangered, reflecting the wider global biodiversity crisis. In response, the field of conservation biology has encompassed palaeontological data, giving rise to conservation palaeobiology. Phylogenetic data can be used to account for bias in studies of extinction selectivity and to test for taxonomic patterns of extinction, particularly whether extinction clusters in certain taxa. Although studies show that extinction risk is not randomly distributed across species, these studies are based on living species only. This leads to a bias in assessments of extinction risk: living groups might seem less threatened because the most susceptible species are already extinct. This project will generate a comprehensive new global phylogeny for Crocodylia that will form the baseline for analysing patterns of extinction in this group. Correlates of extinction susceptibility will be tested, in addition to the taxonomic clustering of extinction. The critically endangered Chinese alligator will be used as a case study. Local ecological information collected from southern Anhui Province, China will be

combined with historical, archaeological and palaeontological data to reconstruct spatiotemporal distribution patterns and assess future threats to reintroduced alligators. This work will demonstrate the application of the fossil record and evolutionary history of organisms to modern conservation and assessing extinction risk today.

THE EARLY TRIASSIC BONE BEDS OF SPITSBERGEN – MARINE ECOSYSTEM RECOVERY AFTER THE P/T EXTINCTION EVENT

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The Early Triassic bone beds of Spitsbergen represent some of the earliest records of marine vertebrate fauna recovery after the Permo-Triassic mass extinction event for the Northern embayment of Pangaea. Limited systematic and stratigraphic control of Early Triassic vertebrate fossils has been undertaken since their discovery in 1860s and as such additional collection and detailed stratigraphic work was required. The Spitsbergen Mesozoic Research Group has over three field seasons collected new material from two of these levels; the *Grippia* niveau and the Lower Saurian niveau, from the Early Triassic (Olenekian) Vendomdalen Member, Vikinghøgda Formation at Marmierfjellet, central Spitsbergen. We present the findings from these excavations with preliminary descriptions of this new material, referable to many known taxa. Both bone beds include large- and small bodied ichthyopterygians, as well as a significant amount of chondrichthyan material. From the Lower Saurian niveau, 571 complete to fragmentary vertebrae and over 750 appendicular and cranial fragments from ichthyopterygians were collected. From the *Grippia* niveau, disarticulated mandibular, rostral and axial skeleton elements from the debated ichthyopterygian genus *Omphalosaurus* were identified. Additionally, this section includes disarticulated skeletons of the poorly understood, small bodied ichthyopterygian *Grippia*. Other vertebrate material from these bone beds include, teeth and cephalic spines from fifteen identified chondrichthyan taxa, as well as teleost, coelacanthian and dipnoi skeletal elements. This material is significant for understanding the faunal recovery at the Northern embayment of Pangaea and for the palaeobiogeographic studies between the Tethys and Panthalassa.

BORED BONES FROM THE TERRESTRIAL MIDDLE CRETACEOUS KEM-KEM BEDS OF SOUTHEAST MOROCCO

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During the last two decades, bioerosion of bone has become more widely investigated, with the earliest identified coming from mid-Triassic strata. Bioerosion has even been identified in bone fragments from a Jurassic theropod coprolite. Although the effects of this destructive process can lead to a loss of important information from the fossil record, understanding of bone bioerosion may be useful for identifying palaeoclimatic conditions in

a variety of ancient fluvial settings.

Recent examination of bones of terrestrial fauna (mostly dinosaurs) from the middle Cretaceous Kem-Kem beds (?Albian–late Cenomanian) of southeast Morocco identified several distinctive bioerosional traces (surface scratches, bite marks [up to 10 cm long] and borings in the form of channels and oval shaped chambers [~5 mm diameter]) from indeterminate producers. One heavily bored bone suggests successive infestation during prolonged subaerial exposure.

Silicon moulding, thin sections and SEM analysis enabled investigation of the bones to determine the producers responsible, and evaluate their role in the taphonomy of ancient fluvial systems.

The bite marks can be attributed to macro predators/scavengers, whereas the borings and surface scratches, are comparable to traces produced by living insects including isopterans and the larvae of coleopterans. Microscopic scratches (approximately 1–2 mm long) within the chambers and channels were also identified and considered fodinichnia and domichnia in the form of pupation chambers.

A NEW MISSISSIPPIAN TETRAPOD FROM FIFE, SCOTLAND, AND ITS ENVIRONMENTAL CONTEXT

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The Viséan stage of the Mississippian is a time of rapid tetrapod diversification which marks the earliest appearance of temnospondyls, microsaurs and the limbless aïstopods. Tetrapod finds from this stage are rare and only a dozen sites are known worldwide. Here we announce the discovery of a new Viséan site in Fife, Scotland. A number of tetrapod taxa are present. The most complete is a new species of the baphetoid *Spathicephalus*, represented by a skull and right mandible. Baphetoids are characterised by large openings on the skull roof, the antorbital vacuities. These are particularly large in the new material. Together the orbits and antorbital vacuities represent approximately 43% of the total skull length. This compares with c. 28% in the younger species *S. mirus* from the Serpukhovian of Scotland. The new specimens represent the oldest known baphetoids, yet belong to the most specialised members of the clade. Unlike typical baphetoids, which have the large marginal teeth and palatal fangs present in most early tetrapods, spathicephalids had very broad, flattened heads, with a dentition consisting of a large number of small, uniform teeth. This suggests that spathicephalids may have fed in a similar way to modern cryptobranchid salamanders, and were the earliest tetrapods to use suction feeding for small, aquatic prey. The associated fauna includes actinopterygians, gyracanthids, lungfish and rhizodonts. These are represented mainly by scales, spines and teeth. Palynological and sedimentological analysis indicates that the new fossil bed was deposited in a large, stratified, freshwater lake that became increasingly saline.

TEMPERATURE AND VARIABLE RATES OF CROCODYLOMORPH BODY SIZE EVOLUTION

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Environmental temperature is an established constraint on the ecology, and geography of ectotherms. Body size interacts closely with temperature through surface area to volume ratio, with direct consequences for physiology. The Crocodylomorpha have shown an enormous diversity of body size, from cat-sized Sphenosuchia to the fearsome *Sarcosuchus*. How does crocodylomorph body size change through time, and how does it relate to climate change? We present an analysis of the interactions between body size, rates of body size evolution and temperature using time-series and comparative phylogenetic approaches. Both body size and rate of body size evolution are found to interact significantly with temperature. Increases in body size and evolutionary rate are associated with periods of cooling, possibly due to constraints imposed by physiology.

VARIABILITY OF THE FOOTPRINTS OF ORIENTAL STORK (*CICONIA BOYCIANA*; AVES, CICONIIDAE) IN HOMOGENEOUS SEDIMENT

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We conducted an ichnological experiment to reveal the morphological variability of *Ciconia boyciana* (Oriental stork) tracks in wet potter's clay. We obtained 54 footprints from two individuals and measured the area, length, width, depth, volume, and rotation for each track. The birds were also filmed while walking. An anatomical feature unique to *C. boyciana* is that, unlike other wading birds, it does not leave metatarsophalangeal pad impressions. This feature can be used to distinguish *C. boyciana* tracks from those left by other birds with similar body weight and habitat. Track width varied by up to 30%, with wider tracks (digits splayed) occurring in trackways with shorter, wider steps. Conversely, narrow trackways with a large stride length were composed of tracks with the toes closer together. Coefficient analysis of track geometry revealed that the width and depth of footprints vary inversely to maintain a consistent volume. Placing the *C. boyciana* footprints into track morphological types (14 types for avians with four digits) yielded the result that most footprints are deeper between digits III and IV than between digits II and III. Combining track data with video footage showing that *C. boyciana* moves its hips from side by side while walking, and noting that the footprints within any given trackway are outwardly rotated, we interpret this track morphology as resulting from laterally directed pressure exerted primarily through Digit IV.

A UNIQUE MORRISON-FORMATION SAUROPOD SPECIMEN WITH BICONCAVE DORSAL VERTEBRAE

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AMNH FARB 291 is a unique sauropod dinosaur specimen, excavated in 1898 from the Bone Cabin Quarry of Wyoming (Upper Jurassic; Morrison Formation). It consists of a sequence of five contiguous dorsal vertebrae, all with biconvex centra: a morphology not previously observed in any sauropod, and which is very rare even in other amniotes.

The specimen was initially catalogued as *Brontosaurus*, one of only half a dozen sauropods then known. But it lacks diplodocid features such as bifid neural spines, short centra and dual centroprezygapophyseal laminae. Instead, it resembles *Brachiosaurus* in its elongated centra, forward-shifted neural arches and lobe-like transverse processes. Centrum lengths (from anteriormost to posteriormost) are 207, 205, 232, 222 and 207 mm, about 60% those of the *Brachiosaurus* holotype.

This specimen could represent: (1) normal development: the condyle would have ossified separately but the individual died before this could happen; (2) a developmental anomaly; (3) a *Brachiosaurus* with a rare variation not previously seen due to paucity of specimens; (4) a bizarre taphonomic event; (5) a unique taxon in which this is a normal, inherited trait.

Vertebrae typically ossify as rings of bone around the notochord, which sometimes persists as a tunnel through the centrum. There is a developmental continuum from biconcave centra with a persistent notochordal tube (as in most fishes), through biconcave centra with the notochord persisting as intervertebral cartilage balls, to the normal amniote condition. However, all known baby sauropod presacrals have already ossified opisthocoelous or amphiplatyan centra, so the present specimen remains mysterious.

GROWTH SERIES OF ONE: CASE STUDIES IN TIME-TRANSGRESSIVE MORPHOLOGY

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The study of ontogeny in the fossil record is complicated by two main factors: growth series are not available for many taxa, and correctly assigning juveniles and adults to the same taxon is often difficult, especially where several related taxa coexisted.

Ontogenetic change can also be revealed in single individuals whose morphology records characters from multiple ontogenetic stages. A snail shell is an intuitive example: the shell grows by accretion at its margin, starting from the larval shell (protoconch), and moving outward. Larval shell shape varies predictably between planktotrophic and non-planktotrophic lineages; and since the protoconch is embedded in the adult shell, larval

ecology can be inferred in adults from the size and morphology of the retained protoconch.

In many extinct lagomorphs, the occlusal surface of the molars changed markedly over the lifespan of an individual, as features such as enamel ridges were revealed and then obliterated by wear. In this case, the complete ‘stack’ of potential occlusal morphologies was present in the adult tooth as soon as it was done mineralizing, and further change progressively erased the ontogenetically early character states.

In sauropodomorph dinosaurs, morphological complexity of the vertebrae increases along the cervical series. The simple morphology of anterior cervicals reflects both earlier ontogenetic stages and more primitive character states. More posterior vertebrae reveal the sequential formation of complex structures.

Individuals that record multiple ontogenetic stages can help solve palaeobiological problems, such as inferring life histories, assessing ranges of variation, and determining the origin of complex morphological characters.